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Behaviour of H- and cutaneous reflexes at different levels of background muscle activity

by

Kathryn Louise Hesketh

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Faculty of Physical Education and Recreation

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Abstract

Two experiments were conducted examining the behaviour of Hoffmann (H-) and cutaneous reflexes under differing levels of background muscle activation during leg cycle ergometry. Participants pedaled at low and high workloads, while reflexes were sampled at one position in the movement cycle (90°- mid way through power phase). Reflexes were also elicited at the same position while participants held static matched Soleus and Tibialis Anterior contraction levels. In experiment 1, Soleus H-reflex amplitudes significantly increased with increasing background muscle activation, but were independent of the type of contraction (static, moving). In experiment 2, cutaneous reflexes did not change with changing muscle activation, but middle latency (70-120 ms) phasic responses in knee extensor muscles showed task-dependent modulation (excitatory during static, inhibitory while moving). Net cutaneous reflexes revealed the same pattern. While H- and cutaneous reflexes show some similarities in reflex behaviour, they seem to be controlled by different factors.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "H- and cutaneous reflex behaviour at different levels of background muscle activity" submitted by Kathryn L. Hesketh in partial fulfillment of the requirements for the degree of Master of Science.

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Dedication

This thesis is dedicated to my grandfathers, W. David Johnston and Gordon Ricker. These two very different men both managed to teach the importance of hard work, dedication and a sense of humour by their examples. I think they would both be very proud of this thesis.

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II. Introduction

It has been pointed out in several papers (e.g., Stein & Capaday, 1988; Zehr & Stein, 1999) that reflexes are not stereotyped responses. While reflexes are commonly perceived as being fixed responses to stimuli, many different factors can influence the response that is elicited. Brooks (1986) described reflexes as being highly probable responses to particular corresponding stimuli. The gain of a reflex is defined as the relation between the size of the stimuli and the size of response it evokes (Yang, Stein, & James, 1991). When the gain of a reflex is high, the magnitude of the response to a given stimulus will be large. When the gain is low, the response to the same stimulus will be of lesser magnitude. Reflex responses can be modulated as a function of movement task, phase and the context in which they are elicited. Thus, for any given level of stimulus input, the magnitude and/or probability of response output can vary depending on factors relating to the current conditions of the system.

While this type of control is more complicated than the popular perception of reflex behaviour, it allows reflexes to be more adaptable and functionally relevant during locomotion and other behaviour. That is, the probability and magnitude of a response is appropriate to the conditions under which the reflex is elicited. For example, during locomotion, reflexes can be tuned up when they will be useful for producing forces during movement, and tuned down when a response might cause a disturbance to balance, or even lead to a fall. What is emerging from the current body of research in this area is that the modulation of reflexes can arise from many different sources. What is not clear is the relative importance of each loci of control under different circumstances.

The stretch reflex (and its electrical analogue the H-reflex) and cutaneous reflexes are two examples amongst a large repertoire of reflexes in the mammalian nervous system. As the behaviour and governance of myotatic and cutaneous reflexes is slowly uncovered, an emergent question of interest is whether all reflex pathways are regulated in the same manner, and if all reflex responses will change in similar ways when elicited under the same conditions.

In the following experiments, H- and cutaneous reflex modulation was studied during cycling movements of the lower limbs. Soleus (SOL) H-reflex modulation has been studied extensively during leg cycling (e.g., Boorman, Becker, Morrice, & Lee, 1992; Brooke, McIlroy, & Collins, 1992; Brown & Kukulka, 1993) and several different possible mechanisms have been examined for their role in controlling the amplitude of the reflex. Although not nearly as documented, cutaneous reflexes have also been studied using a cycling paradigm (Brooke, McIlroy, Staines, Angerilli, & Peritore, 1999; Brown & Kukulka, 1993). Here, H – and cutaneous reflexes were elicited in both static and moving conditions, at low and high levels of background muscle activation. Thus, it was possible to examine the behaviour of both types of reflexes under varying task conditions and motoneuronal excitability, as well as making it possible to compare these two reflex pathways. Additionally, by comparing the reflexes under static and dynamic conditions, it was possible to make inferences about the type of control by which each reflex is governed.

While both types of reflexes have been studied under similar conditions (e.g. Brooke, McIlroy, Staines, Angerilli & Peritore, 1999; McIlroy, Collins & Brooke, 1992), there has never been data collected about both types of reflexes under exactly the same

movement and muscle activity conditions within the same group of participants. This design makes the comparisons of H- and cutaneous reflex behaviour particularly interesting. Differences in the behaviour of the two reflexes can be attributed to differences in the control of the reflex pathways, and not other extraneous variables. In addition, by comparing these two types of reflexes in the same condition, it might also be possible to better understand the contribution each type of reflex makes to rhythmic movement.

The body of this thesis is divided into three sections. In the basic concepts section, concepts central to understanding reflex neurophysiology are provided for readers who are unfamiliar with the area. In addition, some topics are covered to give the reader background for the rationale behind much of the experimental set-up. For further assistance, a supplementary glossary is provided at the end of the thesis. The review of literature section provides a brief synopsis of the relevant research to date in this area. This section is intended to help the reader understand the rationale for the questions addressed in the third section: the experiments. As well as a description of methods and procedures, the experiments section provides a discussion of the experimental results specific to each experiment and the overall picture of the findings.

III. Basic concepts

A. Sensory receptors

There are several different types of sensory receptors in humans. Of relevance to this set of experiments are those receptors sensitive to cutaneous, intramuscular or intracapsular (within the joint capsular) sensations like stretch, pressure and tension.

The information detected by the sensory receptors is transmitted via sensory afferents. These are the nervous tissues that conduct sensory stimuli to the spinal cord. Afferent fibres can be classified using different methods: electrical properties and conduction velocity. Generally, sensory fibres supplying muscles and skin are referred to using Group I, II, III and IV fibres. Group I fibres are the largest, most myelinated fibres (thickest myelin sheath) and the highest conduction velocity. Groups II and III are smaller and less myelinated (thinner myelin sheath). Group IV fibres are unmyelinated have the slowest conduction velocity (Nicholls, Martin & Wallace, 1992). These groups can be further differentiated according to the type of sensory receptor they innervate, thus producing names like Ia and Ib.

i. Muscle spindles

The primary endings of the muscle spindles transmit sensory information from static and dynamic bag and chain fibres in the muscle spindle to the spinal cord. Thus, Ia afferents are sensitive to the amount (from static bag and chain) and the rate of stretch (from dynamic bag) of the intrafusal fibres. Primary spindle endings are located centrally on the intrafusal fibres. Ia fibres are thickly myelinated, and thus have the highest conduction velocity of the sensory fibres (Nicholls et al., 1992). Their large size is also advantageous to researchers interested in studying the H-reflex, since low level electrical stimulation will differentially excite the Ia axons first, without exciting other sensory or motor fibres (Schieppati, 1988).

The sensitivity of the muscle spindles is controlled by the γ-motor system. Separate from the α-motor system which innervates extrafusal muscle fibres, the γ- or fusimotor system innervates the intrafusal fibres inside the capsule of the spindle.

Increasing fusimotor drive stretches the elastic central portion of the intrafusal fibres (where the bag and chain fibres are located), which increases the sensitivity of the primary and secondary endings to stretch (Nicholls et al., 1992).

Also present in the muscle spindle are secondary sensory endings. Located peripherally on one or both sides of the primary endings, these receptors are sensitive to the length of the muscle fibre, but do not respond to dynamic change in muscle length (innervating only the static bag and chain fibres). Secondary endings are innervated by group II fibres, which are smaller than group I fibres and require a greater intensity electrical stimulation to be activated (Nicholls et al., 1992).

ii. Golgi tendon organs

Ib afferents innervate the tension-detecting tendon organs. Ib fibres are smaller than Ia fibres. Golgi tendon organs are located at the musculo-tendinous junction, and are activated when their endings are squeezed when muscular force is developed. Individual tendon organs detect force; however, the actual variation in tension being generated in a given muscle is reflected only in the ensemble discharge of all of the tendon organs in that muscle (Jami, Petit, Proske & Zytnicki, 1985).

iii. Cutaneous mechanoreceptors

Cutaneous mechanoreceptors respond to deformation of the skin . Merkel's disks are slowly adapting pressure receptors. Meissner corpuscles are found near the surface of the skin and are rapidly adapting and sensitive to stroking and fluttering stimuli on the skin surface. Both Merkel's disks and Meissner corpuscles are found in the superficial layers of the skin. Pacinian corpuscles are located deeper in the skin layers and are sensitive to vibration. Ruffini endings are also found in the deeper cutaneous layers. Similar to

Meissner's corpuscles in structure, they too detect stroking and fluttering stimuli, and are highly rapidly adapting. Group II afferent fibres innervate these types of receptors (Kandel, Schwartz & Gessell, 2000).

B. Basics of the reflex pathway

The general anatomy of a basic reflex pathway consists of a simple circuit. In reflexes elicited under natural circumstances, a disturbance is detected by a mechanoreceptor (stretch receptor, tension receptor, cutaneous mechanoreceptor) that transduces the mechanical signal into an electrical impulse. In a monosynaptic reflex, the signal is transmitted via sensory afferent fibres (through the dorsal horn of the spinal cord) to synapse onto a α-motoneuron in the anterior horn of the spinal cord. In a di-,or polysynaptic reflex, the signal will be transmitted via one or several interneurons. While the information transmitted to the spinal cord is relayed via ascending tracts to higher centres in the brain and brainstem, a reflex response is evoked through the motoneuronal pool, effecting an overt muscle response. Typically a small rapid muscle contraction is the response in the case of a stretch or H-reflex (Figure 1). In the case of the classic "tendon jerk" reflex, a tap on the tendon stretches the associated muscle which is detected by the muscle spindles. This information is transmitted via the sensory afferents to the α-motoneurons, which in turn causes a contraction of the homonymous muscle in response to the stretch. This type of simple reflex illustrates the type of circuitry involved in other more complicated reflexes, like the crossed-extensor reflex. In the crossed extensor reflex, painful stimulation of the ipsilateral leg causes withdrawal of the leg from a stimulus, as well as causing the contralateral leg to extend forcefully, in order to maintain support and balance while the ipsilateral leg is off the ground. The crossed-extensor reflex is an

example of a reflex that uses the same type of simple arrangement as a basis, but uses interneurons to convey information between pathways to produce a far more complex reflex response.

C. Commonly studied types of reflexes

i. Myotatic reflexes

a. Stretch reflex

The stretch reflex results from the activation of the primary endings of the muscle spindles. A small rapid stretch to the muscle stretches the intrafusal fibres of the muscle spindle. The increase in annulospiral primary spindle ending firing rates are transmitted through the Ia afferents, which, in turn, synapse onto the α-motoneurons and cause a rapid muscle contraction in response to the imposed stretch.

In an experimental setting, rapid muscle stretch can be applied using an actuator, a brace-like device that can transduce joint ankle at the joint it is positioned. At the desired joint position, the actuator rapidly moves the joint, imposing a stretch on the target muscle (Sinkjaer, Andersen & Larsen, 1996; Yang, Stein & James, 1991).

The stretch reflex has many important implications for the maintenance of balance and gait. Stretch reflexes may help maintain balance by compensating for perturbations arising from irregularities in the walking surface during gait (Dietz, 1992). The SOL stretch reflex has been proposed to contribute to support during early stance phase during gait, as the triceps surae is stretched when body weight shifts onto the leg (Sinkjaer et al, 1996). Control of the stretch reflex is also thought to be critical for voluntary movement. The velocity-dependent threshold at which antagonist muscles are activated to oppose

stretch must increase, in order to reduce co-contraction and allow joint movement through a full range of motion (Sinkjaer et al, 1996).

b. The Hoffmann Reflex

The Hoffmann (or H-) reflex is an artificially elicited reflex observed when a mixed nerve is stimulated with a small electrical impulse. A small impulse will excite the large Ia afferents, which synapse with α-motoneurons innervating the muscle. The response latency of the reflex is about 35-45 msec (Schieppati, 1987), and it is most likely a monosynaptic reflex (Stein & Capaday, 1988) (Figure 2). However, the contribution of polysynaptic pathways gives the reflex waveform its characteristic shape (Stein, 1995).

Before the onset of the H-reflex, an initial response called the M-wave is seen with an average latency of 5 milliseconds (Schieppati, 1987). The M-wave is a result of some motor axons being stimulated directly in a mixed nerve, and is of great methodological importance. Unlike the H-reflex, which is susceptible to modulation under varying conditions, the amplitude of the M-wave is based solely on the magnitude of the stimulus input (Crenna & Frigo, 1987). Thus, it can be assumed that if the M-wave amplitude is constant, then the same percentage of the motor axons are being excited (and presumably a constant percentage of sensory fibres) (Stein & Capaday, 1988). An additional part of this assumption is that sensory and motor axons are distributed uniformly within the mixed nerve trunk.

In the majority of reflex modulation studies, the M-wave is used as a control, to ensure that stimuli are of constant magnitude during experimentation (e.g., Brooke et al., 1992; Cheng, Brooke, Misiaszek, & Staines, 1998; Misiaszek, Brooke, Lafferty, Cheng, & Staines, 1995; Misiaszek & Pearson, 1997). However, sometimes a consistent-sized M-

wave is difficult to obtain due to the vigorous nature of the activity being performed. In some cases, electrode placement relative to the nerve will change as the skin and adipose tissue move during the activity, changing the input the nerve receives while the electrode remains in a fixed position on the skin. In cases in which this movement cannot be controlled, an M-wave-H-reflex curve can be generated at each position of interest (Figure 3). Stimuli of intensities varying between M threshold to M_{max} (the largest M amplitude that can be elicited) are delivered to the nerve. The M-H pairs are subsequently ordered (smallest to largest M-wave). A regression line can then be calculated to fit the data points. This line can be used to infer the relationship between electrical input and reflex output at a given limb position (Stein & Capaday, 1988; Zehr & Stein, 1999a).

c. Comparison of stretch and H-reflex

The H-reflex is often described as the electrical analogue to the stretch reflex, since they are both caused by stimulation of the Ia afferents. The H-reflex follows the same pathway as the stretch reflex, but bypasses the muscle spindles. Thus, the stretch reflex is sensitive to γ-drive, but the H-reflex is not. Studies using the H-reflex do not necessarily find the same results as studies using the stretch reflex.

The gain of stretch reflexes is thought to be at least partially controlled by γ-drive. In a recent study of stretch and H-reflexes during two-legged hopping, there was a significant negative correlation between the amplitude of soleus stretch reflexes and the estimated peak velocity of muscle spindle shortening, so the relationship between reflex amplitude and rate of stretch was reversed during movement. However, soleus H-reflexes did not show the same pattern as stretch reflexes. This finding suggests changing fusimotor drive is modifying sensitivity of the muscle spindles (Voigt et al., 1998). Some

research suggests that the similarities between the H- and stretch reflexes indicate an at most, modest contribution of fusimotor influence on the stretch reflex (Prochazka, Westerman & Ziccone, 1977). Other authors have suggested that the rapidity of changes to the gain of the stretch reflex would exclude γ-drive as a possible mechanism, and that other peripheral and supraspinal inputs are more likely candidates for the control mechanism (Kirsch & Kearney, 1993; Sinkjaer et al., 1996).

In soleus, H-reflex is more sensitive to presynaptic inhibition caused by biceps femoris vibration than is the stretch reflex elicited by passive stretch (Morita, Petersen, Christensen, Sinkjær & Nielsen, 1998). The H-reflex is elicited by a relatively large, short duration, synchronous afferent volley, while the stretch reflex stimulus is smaller, of longer duration, and the afferent volley to the spinal cord is more dispersed in time. It is unlikely that changing fusimotor drive causes the difference between the reflexes, since the effects are long lasting (Morita et al., 1998). It is prudent to consider this finding and the others noted above when trying to draw conclusions about stretch reflex behaviour while using the H-reflex as an experimental tool.

While the H-reflex is an electrically evoked reflex (and thus artificial), it is an important means of studying muscle reflex pathways, and the contribution of reflexes to movement. The stretch reflex is a more ecologically relevant reflex to study, because it is elicited by a naturally occurring input. It is sometimes methodologically impractical to evoke a stretch reflex during movement. Adding to the problem is difficulty in estimating rates of muscle spindle stretch, making interpretation of results difficult (Voigt, Dyhre-Poulsen & Simonsen, 1998). The H-reflex, on the other hand, is relatively easy to elicit. For all of these reasons, the H-reflex is often a more practical means of studying the

different mechanisms that might be responsible for controlling muscle reflexes during movement. When compared with results using the H-reflex, the stretch reflex showed similar patterns of modulation during gait (Stein, Yang, Bélanger & Pearson, 1993; cf. Sinkjær et al, 1996). Thus, the H-reflex is a useful tool for exploring reflex pathways during rhythmic movement. More generally, the control of myotatic reflexes has important implications in understanding basic neural control during movement.

ii. Cutaneous reflexes

Cutaneous reflexes occur as a result of stimulation of tactile receptors in the skin. In an experimental setting, generally a short, high frequency train of 3-5 stimuli (200-300 Hz with pulse width 1 ms) are applied to a nerve to elicit a reflex (Christensen, Morita, Petersen, & Nielsen, 1999;Van Wezel, Ottenhoff, & Duysens, 1997; Zehr & Stein, 1999). However, it is also possible to use techniques such as mechanical tapping or brushing. To date, the majority of research into cutaneous reflexes during rhythmic movement has involved various nerves and areas of the foot and lower leg. (e.g., De Serres, Yang & Patrick , 1995; Van Wezel et al, 1997; Zehr, Komiyama & Stein, 1997)

Cutaneous responses are highly complex. They can involve one or several consecutive periods of inhibition and excitation at varying latencies (Figure 4). Generally, responses have been categorized on the basis of latency as early, middle and late responses to stimuli. The latency of responses is dependent on both the nerve which is stimulated and the muscle in which the reflex in measured. Tibial nerve, which innervates the foot sole, has been shown to have early latency or P1 (nomenclature from animal research) responses, are generally those with latencies of less than 65 milliseconds in the leg muscles (Brooke, Cheng, Collins, McIlroy, Misiaszek & Staines, 1997). Middle (P2) responses

are those that occur between 70 and 120 milliseconds (Cheng et al., 1997) and late (P3) are responses with a latency greater than 130 milliseconds. Middle latency responses are typically the responses which change reliably with changing contextual requirements, and are thus the response on which most research and speculation has been focused (Duysens, Tax, Murrer & Dietz, 1996; Duysens, Tax, Trippel & Dietz, 1993; Duysens, Trippel, Horstmann & Dietz, 1990; Tax , Van Wezel, & Dietz, 1995; Yang & Stein, 1990).

While some researchers have focused on describing the pattern of excitation and inhibition, others have used a more global variable that describes the nature of the response in general. A post-stimulus time histogram (PSTH) is one such measure. A PSTH gives an overall idea of the timing and magnitude of the reflex response as well as a measure of synaptic input to single motoneurons (DeSerres, Yang & Patrick, 1995). Another measurement, the Average Cumulative Reflex EMG (ACRE) is an integrated average of the EMG response over a specific period of time. Usually 150 ms after the first stimulus in a train is used to calculate $ACRE_{150}$. The intention of such a variable is to characterize the general response, and thus give some insight into what the net effect of the reflex might be on limb kinematics. The argument against using such a variable is that information about individual parts of the response is lost (Zehr & Stein, 1999b).

Eliciting electrically induced cutaneous reflexes has the same drawbacks when making inferences to normal reflex behaviour as does using the H-reflex to make inferences about stretch reflexes. Electrical stimulation of afferents causes a more synchronous activation of pathways than does a normal tactile stimulation such as brushing or stroking an area of skin. However, using electrical stimulation can still be

useful in examining the cutaneous pathways and the mechanisms that change them during movement (Duysens Tax, Trippel & Dietz, 1992).

D. Presynaptic inhibition and primary afferent depolarization

Presynaptic inhibition (and excitation) is the result of axo-axonic (and also axo-dendritic) synapses. In a given reflex pathway, any time there is a synapse between neurons in the pathway, there is the possibility of input from other pathways in the peripheral nervous system. Interneurons can synapse onto either the presynaptic axon terminals or postsynaptic cell body, producing a net effect of either excitation or inhibition, depending on the type of synapse. Presynaptic inputs alter the amount of neurotransmitter released into the synaptic cleft, thereby affecting the output of the postsynaptic cell. Postsynaptic synapses changes the properties of the postsynaptic cell to alter the probability of it firing at a given level of input (neurotransmitter).

The size of a reflex response to a given stimulus is dependent on two factors; 1) the current state of excitability of the motoneuron pool, and 2) the degree of pre- and postsynaptic influences on the inputs to the motoneurons (Brooke et al., 1997; Pierrot-Deseilligny, 1997; Stein & Capaday, 1988; Yang & Whelan, 1993). While postsynaptic inhibition can affect the amplitude of a reflex, it will also modulate background EMG activity. Presynaptic inhibition, on the other hand, will modulate excitability independently of background EMG (Stein, 1995). In order to study the effects of presynaptic inhibition, it is therefore necessary to make comparisons of reflex amplitude at similar levels of EMG activity. For example, when comparisons were made between standing, walking and running, with similar levels of background EMG, Capaday and Stein (1986) reported that the degree of H-reflex suppression in soleus was significantly greater in walking than

standing, and greater still in running. Edamura et al. (1991) reported a similar finding when making comparisons of walking and running at equivalent levels of EMG activity, with running showing greater inhibitory effects than walking (see Figure 6).

The mechanism by which presynaptic inhibition is thought to act is known as primary afferent depolarization (PAD). PAD occurs when an inhibitory interneuron acts on the target presynaptic terminal to depolarize the terminal bouton and reduce the efficacy of any arriving action potential. Presynaptic inhibition occurs when an inhibitory interneuron synapses onto a presynaptic axon terminal and blocks the release of transmitter to the postsynaptic neuron by depolarizing the terminal (PAD) before the action potential arrives (Figure 5). The inhibitory interneurons release GABA (see Glossary)- an inhibitory neurotransmitter. The efficacy of the action potential is diminished due to shunting and it does not open as many high-threshold calcium channels to signal neurotransmitter release. Thus, the size of the postsynaptic potential in the presence of presynaptic inhibition is smaller than when presynaptic inhibition is not present. If inhibitory interneurons are active when a reflex is elicited, the gain of the reflex will tend to be smaller because the amount of neurotransmitter released from the presynaptic terminal is reduced. The summed potential that reaches the motoneuron that innervates the muscle is smaller and is less likely to cause the motoneuron to reach threshold and fire. This is different from the excitability of the motoneuron pool, which is represented by the probability of a given input producing an action potential. Functionally, presynaptic inhibition provides the nervous system with the ability to control the relative weighting of the influence of input from a specific afferent source (e.g., stretch or load receptors) on to a neural pathway (e.g., reflex arc), resulting in fine-tuned control of reflexes and voluntary

movement (Dietz, 1992).

E. Central pattern generators and reflex reversals

Central pattern generators (CPG) are one possible mechanism that may influence reflexes during rhythmic movement. The general notion of a central pattern generator is that of a group of neurons and interneurons that act to generate specific stereotyped movements, and can act even in the absence of descending or afferent feedback. CPGs for stereotypical movements such as respiration, mastication, swimming and gait in insects and some more primitive vertebrates have been studied extensively, mostly in reduced preparations (Cohen, Rossignol & Grillner, 1988). The small amount of direct empirical evidence for the presence of CPGs in humans has come from experiments using persons with complete spinal cord injuries as participants. With strong electrical stimulation to the spinal cord, it is possible to generate alternating rhythmic patterns of leg muscle activity in people with complete spinal cord transection (i.e., no descending input)(Dimitrijevic, Gerasimenko and Pinter, 1998). Whether or not CPGs in the form found in other animals exist in humans is a contentious issue.

Activated by the structures in the brainstem, a CPG is hypothesized to function by selecting appropriate afferent input from the environment and tune movement so that it meets current environmental requirements (Grillner, 1981). These centres are thought to be able to modulate peripheral input so that a given input is either amplified or filtered, depending on the context (e.g., phase of the movement) (Dietz, 1992). As a result, reflexes that are evoked by this afferent input is appropriate to the conditions under which they are elicited. Converging spinal pathways and interneurons allow for a complex interplay of many central and peripheral influences on the motoneurons.

One form of reflex behaviour that CPGs are believed to control is reflex reversals. In their strictest definition, reflex reversals are a specific form of phase-dependent reflex modulation. In order to be defined as a reflex reversal, a stimulus of a given intensity must induce a reflex response in flexors during one phase of movement, but induce a reflex of the same sign and latency in extensors at another phase of the movement (Duysens et al., 1990). Another type of reflex reversal is a change in sign of a reflex response in one muscle, depending on the phase of movement. For example, reflex reversals in TA have been observed during walking, with TA response being excitatory Yang & Stein, 1990) during swing, and inhibitory during stance. Reflex reversals seem to arise as a result of a CPG, since they have been shown to occur during fictive locomotion (i.e., no afferent input) in paralysed cats (Andersson, Forssberg, Grillner, & Lindquist, 1978). However, afferent input may also play a role in reflex modulation, since reflex reversals were observed during static flexion and extension contractions (Grillner & Rossignol, 1978).

F. Extraneous factors that can affect reflexes

i. Joint position

Joint position can influence reflex modulation by affecting sensory afferent discharge from group Ib and II (innervating Golgi tendon organs and secondary spindle endings) as well as other sensory receptors (like cutaneous receptors that detect stretch in the skin around the joint) which in turn influence reflex size. Turker, Seguin and Miles (1989) observed significant differences in inhibitory reflexes in the human masseter muscle as the jaw was held in a range of positions with a tonic level of excitation in the motor units under investigation. Similarly, Evans, Harrison and Stephens (1989) compared cutaneous reflex responses while subjects held various static hand positions. Their investigation of task-

dependent changes to the reflex was arguably also an investigation of joint position, since it was the factor that changed between tasks. Small changes in inhibitory cutaneous responses were seen, depending on the hand positioning (Evans et al., 1989).

The H-reflex has also been shown to be influenced by joint position. Reciprocal inhibition of the ankle flexors onto the ankle extensors was observed to change depending on the ankle angle (Shindo, Harayama, Kondo, Yanagisawa & Tanaka, 1984). The size of the H-reflex increased with dorsi flexion, and decreased or was completely abolished during plantar flexion. Thus, it is important to control joint angle when making comparisons of reflex amplitude while varying other factors.

ii. Jendrassik maneuver

Named for Ernst Jendrássik (1883), the Jendrássik maneuver (JM) refers to the contraction of upper limb and facial muscles, resulting in facilitation of reflexes in the lower limbs (Zehr & Stein, 1999a). To contract these muscles isometrically, experimental participants are instructed to clasp their hands together and pull in opposite directions, as well as to clench their teeth, both with near maximal effort (Burke, McKeon & Westerman, 1980). The maneuver was first noted to potentiate stretch reflexes, and it was thought that the afference from the upper limbs was increasing fusimotor drive to the spindles in the lower limbs. However, Hagbarth, Wallin, Burke and Löfstedt (1975) demonstrated that the change in response from the spindles was more closely related to changes in the extrafusal muscle. Burke et al. (1980) found that the JM did not increase fusimotor drive to individual spindles. It was also found that JM potentiated the H-reflex, even under ischemic conditions, when feedback from the spindles was blocked (Bussel,

Morin & Pierrot-Deseilligny, 1978). Thus the Jendrássik maneuver does not activate the gamma motor system.

More recent study of JM observed that at constant EMG levels (and thus stable motoneuron excitability), JM facilitated H-reflex in soleus, as well as reducing pre-synaptic inhibition elicited from stimulation applied to the antagonist CP nerve (Zehr & Stein, 1999b). The authors suggest that the outflow resulting from JM acts to inhibit the inhibitory interneurons that would normally cause presynaptic inhibition of the reflex. Because of the strong effects these pathways can exert, it is important to monitor the activity in the upper limbs during reflex experiments in the lower limbs, particularly as the activity involves higher levels of muscular effort.

While the effect of JM on H-reflex is well documented, no such investigation of the relationship of JM with cutaneous reflexes has been published to date.

iii. Fatigue

The majority of experimentation on the H-reflex during rhythmic activity has been under conditions that allow the subject either to cycle or run at a fairly moderate and comfortable pace and intensity. However, activities such as cycling and running are often done for long periods of time and the participants are susceptible to fatigue. Therefore, it is relevant to know how the H-reflex and M-wave behave under fatiguing conditions. Garland (1991) found that during sustained maximum voluntary contractions, under ischemic conditions, the H-reflex is almost entirely abolished. There was a 93% decrease in the peak-to-peak amplitude of the H-reflex when compared to control values. A 56% decrease in EMG activity and a 36% decrease in maximum plantar flexion torque generated by the soleus accompanied the attenuation of the H-reflex. The M-wave, on the

other hand, showed no significant changes with fatigue. Similar results were found in soleus when voluntary contractions were used to fatigue the muscle, but not with electrical stimulation causing muscular fatigue (Tsuboi, Sato, Egawa & Miyazaki, 1995). Behm and St. Pierre (1997) did find a decrease in M-wave amplitude during long duration isometric contractions (20 minutes) of the soleus, but found potentiation of the M-wave in the more rapidly fatiguing quadriceps muscles. In experiments using the finger muscles adductor pollicis brevis and first dorsal interosseous, a 30% decrease in H-reflex during sustained maximum voluntary contractions was seen, while no such decrement was seen in long latency reflexes (Duchateau & Hainaut, 1993). They also noted that the long latency reflex was facilitated in one muscle when the other muscle was fatigued. This suggests that during fatigue, an increase in central drive was used to compensate for the local loss of excitation.

A recent experiment by Crone, Johnsen, Hultborn, and Orsnes (1999) is of great methodological importance to the present set of experiments. They studied the peak-to-peak amplitude of M_{max} and H_{max} elicited over an experimental time period of one to three hours in participants at rest. Both M_{max} and H_{max} decreased significantly over periods as short as ten minutes. However, both M and H decreased proportionally the same amount (20.5% decrease in M_{max} and 19.1% decrease in H_{max}), so the ratio between the two values remains constant. However, since a majority of experiments use M_{max} to standardize H- and M-amplitudes across conditions, it is important to ensure that each condition within an experiment is normalized with an M_{max} value that has been collected within close temporal proximity. Crone et al. (1999) also noted that the decrease was not observed in participants who had exercised in the hour previous to testing. Thus previous muscle

activity may prevent the decrease in H and M size. This idea is not yet substantiated experimentally. No published experiments to date have examined the effect of the length of experimental sessions on cutaneous reflexes.

IV. Review of Literature

A. Modulation of H- and cutaneous reflexes

i. Static conditions

During static contraction, the magnitude of a cutaneous reflex response is found to be linearly related to the activation level of the muscle (Burke, Dickson, Skuse, 1991; Zehr, Komiyama & Stein, 1997). However, Grillner and Rossignol (1978a) reported position-dependent modulation of cutaneous reflexes during static leg positioning in decerebrate cats. Stimulation was applied to one leg, which was held in a constant position. Recordings were made from the contralateral leg. When the contralateral leg was flexed, bursts of activity were observed in quadriceps and gastrocnemius, while antagonist muscles were quiescent. When the contralateral leg was fully extended, activity was seen in semitendinosus and TA, but quadriceps and gastrocnemius were silent (a reflex reversal).

Burke et al. (1991) observed differences in short latency (60-80 ms) cutaneous responses when comparing various static stable and unstable postures. When standing with the toes pointing up, TA activity was high, and TA reflex responses were large. Meanwhile, SOL was very quiet. When the toes were tilted down, SOL activity and cutaneous reflex responses were highly excitatory, while there was almost no activity in

TA. These differences in response according to position contribute to the maintenance of the existing static posture.

Funase and Miles (1999) examined H-reflex responses in SOL during static isometric contractions. They observed that the H-reflex size was dependent on background EMG at the time that the H-reflex was elicited, but only at high levels of muscle contraction. During low levels of contraction, the relation between H-reflex amplitude and background muscle activity was small or non-existent.

ii. Walking

There is a general pattern of SOL H-reflex modulation observed during the walking cycle. There is a mild facilitation in SOL during stance phase, followed by a period of response attenuation during swing phase. The H-reflex depression continues through to the swing-to-stance transition, then once again becomes a facilitation (Crenna & Frigo, 1987). This modulation follows the same type of pattern during cycling, where the gain of the H-reflex is highest while soleus is contracting, and lowest while it is relaxing. However, passive stepping has also shown inhibition of the soleus H-reflex, with a constant inhibition throughout the step cycle (Brooke, Cheng, Misiaszek, & Lafferty, 1995). Yang and Whelan (1993) trained participants to walk while activating soleus during swing phase (when normally quiet) in one condition, and to keep tibialis anterior (the antagonist muscle to soleus) quiet during gait in another condition. The change in muscle activity did not account for the modulation pattern seen throughout the step cycle. Similarly, in a study of the stretch reflex in triceps surae, Weiss et al. (1986) noted that the reflex amplitude increased with increasing tonic EMG activity, but also found that peak-

to-peak reflex amplitude increased with increasing dorsiflexion of the ankle. The stretch reflex amplitude was up to 25 times greater when the ankle was in a maximally dorsiflexed position than when in a neutral position. However, they did not find the same position-dependence in tibialis anterior.

Crenna and Frigo (1987) noted that the relative magnitude of the H-reflex during the step cycle closely matched EMG levels during each phase. However, several studies have shown that H-reflex modulation is independent of levels of muscular activity (Brooke et al., 1995; Edamura et al., 1991; Lavoie, Devanne & Capaday, 1997; Yang & Whelan, 1993). Brooke and colleagues (1995) demonstrated that the H-reflex can be inhibited while the muscles are quiet during passive walking and stepping. Cheng, Brooke, Staines, Misiaszek and Hoare (1995b) observed that if muscles are tonically contracted during passive movement, phase-dependent modulation is still seen despite constant muscle activity level. Phase-dependent modulation was also observed in static conditions, when no muscle activity was present (Cheng et al., 1995b). Other studies by Capaday and Stein (1986, 1987) found that the level of attenuation of the reflex was different for different tasks (standing, walking and running). Thus, the response elicited was different depending on the task, even with the same level of activity in soleus muscle (see Fig. 6). Similarly, increased activation of the soleus during the swing phase of walking did not affect the suppression of the H-reflex (Yang & Whelan, 1993).

During locomotion in the cat, cutaneous reflexes are facilitated in flexors and inhibited in extensors when a stimuli is delivered to the foot sole during swing phase (Forssberg, Grillner & Rossignol, 1975; Forssberg, 1979). During stance phase, the

pattern of excitation and inhibition is reversed. This phenomenon is known as "phase-dependent reflex reversal", and has been reported in cats (Forssberg et al., 1975), as well as humans (Bélanger & , 1987; Yang & Stein, 1990).

Yang and Stein (1990), observed reflex reversals in TA during human walking. During swing phase, an excitatory response was elicited, until the stance-to-swing-transition, when the response reversed and was inhibitory. Responses continued to be inhibitory during stance phase. In SOL, responses were more variable, but did show a similar (reversed) pattern, with excitation during swing phase and early stance, with inhibition in late stance in some participants. Duysens et al., (1990) also reported reflex reversals during human walking when comparing TA and MG muscles.

Comparisons of cutaneous reflexes between walking and standing reveal a different pattern of reflex behaviour than that previously observed in the H-reflex, Komiyama, Zehr and Stein (in press) found that during standing, cutaneous reflexes in lower leg muscles were suppresive when stimulation was applied to various cutaneous nerves, and that the degree of inhibition was greater with increasing background muscle activity. However, during walking, reflexes were facilitated, independent of background muscle activity. This behaviour is opposite to the H-reflex, which tends to become smaller when moving from static contractions to gait (Capaday & Stein, 1986).

iii. Running

Running shows a similar pattern of phase-dependent modulation of the H-reflex to that observed during walking. The H-reflex is almost completely absent during swing phase and the initial part of stance, then builds up gradually to a maximum late in stance

phase. When compared with walking, there is significantly more inhibition of soleus H-reflex during running, despite levels of EMG activity which are 2.4 times greater during running (Capaday & Stein, 1987). Edamura et al. (1991) found that the mode of locomotion had a much greater influence on gain of the reflex than did the speed of movement. Within a mode, the greater the velocity of movement, the lower the gain of the H-reflex.

Dietz, Schmidtbleicher and Noth (1979) suggested previously that stretch reflexes contribute significantly to triceps surae force production in late stance phase during sprinting. Similarly, Yang et al. (1991) estimated that stretch reflexes were responsible for 30-60% of total activation of soleus during the early stance phase of walking.

If reflexes are important for force production, why are they smaller during running, when larger forces are being produced, than during walking? One suggestion is that the modulation occurs to decrease the likelihood of an inappropriate stretch reflex response (Capaday & Stein, 1987; Edamura et al., 1991; Yang & Whelan, 1993). During swing phase, the foot is dorsi-flexed and if the gain of the stretch reflex in soleus were higher during running, people could be more likely to trip, because a small stretch to soleus would cause the foot to plantarflex suddenly. Additionally, when comparing running to walking, running generally occurs at higher velocities, thus a reflex response with a given latency (40 or so milliseconds) will occur proportionally later in the step cycle during running versus walking. Thus, the speed of the step cycle during running makes it less useful to elicit large corrective reflexes.

A recent paper by Simonsen and Dyhre-Poulsen (1999) re-examined the often-cited findings of Capaday and Stein (1987). Using both the earlier paper's method of

analysis in addition to a new method, the H-reflex was significantly inhibited during swing phase and facilitated in stance phase during walking and running at different velocities. However, they did not find significant differences in H-reflex amplitude across gait mode or velocity of movement (walking and running at three velocities). Simonsen and Dyhre-Poulsen suggest that the suppression in H-reflex during running that they found is useful to prevent saturation of the motoneuron pool that might lead to problems such as tremor. However, Simonsen and Dyhre-Poulsen (1999) conclude that saturation is not likely to become an issue, since their subjects ran at velocities faster (with presumably a greater excitability of the motoneuron pool) than did the subjects in the Capaday and Stein experiment without experiencing saturation (manifested in tremor). Simonsen and Dyhre-Poulsen (1999) argue that the H-reflex should not be suppressed during running, so that the stretch reflex can be utilized to increase muscle stiffness and increase running efficiency (see also Dietz et al., 1979).

Cutaneous reflexes are also subject to phase-dependent modulation during running. Duysens, Tax, Trippel and Dietz (1992) observed excitatory responses to low –intensity stimuli in TA during early swing, which became smaller and eventually reversed to inhibitory responses in late swing and during stance. The changes in TA reflex response were accompanied by corresponding change in ankle angle (greater dorsiflexion during swing phase, less dorsiflexion during stance phase). The correlation between the two events suggests that the cutaneous responses resulted in altered gait kinematics during disturbed walking.

In addition to phasic gain control, task-specific modulation of cutaneous reflexes has been observed in a comparison of standing and running. However, unlike the H-reflex, the amplitude of the cutaneous responses increased from standing to running (Duysens et al., 1993). Kanda and Sato (1983) reported similar, albeit weaker, phase-dependent reflex responses in hamstrings and quadriceps to sural nerve stimulation during stepping movements, and the absence of any response during quiet standing.

The functional implication of this flexibility is that stimulation of different regions of the foot (sole, dorsum) during locomotion results in a response that is appropriate depending on the context in which it is elicited. Stimulation of one nerve may induce facilitation in a flexor and an inhibitory response in the corresponding extensor muscle during one phase of movement, but will produce the reverse response at a later stage of movement, exciting the extensor and suppressing the flexor (reflex reversal). More importantly, the pattern of excitation and inhibition that is produced has been shown to produce observable changes in limb kinematics during gait (Zehr, Komiyama, & Stein, 1997; Zehr et al., 1998). Cutaneous reflexes then appear to make meaningful contributions to altering gait patterns.

iv. Leg Cycling

Just as in walking and running, phase-dependent modulation of the H-reflex has been observed during cycling. The soleus H-reflex is largest during the downstroke (or knee extension phase) of the crank cycle, reaching a peak at about at 90° of the cycle (midway through downstroke). The H-reflex is almost abolished during the recovery (or knee flexion) phase of the movement, until around 270% of the crank cycle (midway

through recovery (Brooke et al., 1992) (see Figure 7)). Boorman et al. (1992) noted similar findings during studies of persons who are neurologically intact, but not of participants with incomplete spinal cord injuries (SCI). These findings coincide with later work by Brooke et al. (1997) which showed that the highest gain in soleus H-reflex was observed when soleus was most active. Stewart and Brooke (1993) had participants make rapid plantar-flexion movements, and found that there was a facilitation of the H-reflex, both prior to and after movement onset. H-responses elicited 60 milliseconds prior to movement were shown to be 36% larger than the magnitude of the control responses. Thus, not only does activation of the soleus muscle affect the size of the reflex, but anticipation of muscle activation also facilitated the H-reflex size . This phenomenon points to at least some effect of supraspinal drive in reflex modulation.

McIlroy, Collins and Brooke (1992) observed an association between cycling cadence and H-reflex depression. They found that the higher the pedaling frequency, the more depressed the elicited H-reflexes were. The same held true even if the legs were pedaled passively. Boorman et al. (1992) found that there was little modulation of the H-reflex with passive pedaling, but used very low cadence (20 rpm vs. Brooke's group using 60 rpm). Both groups observed that the degree of velocity-dependent depression was not related to phase and thus was independent of the level of activity in the soleus muscle. Reflexes have been found to be phase-modulated during slow passive cycling and passive placement of the leg at various points in the cycle (Cheng, Brooke, Misiaszek, & Staines, 1995a).

Boorman et al. (1992) reported an increase in the amplitude of the H-reflex with increasing workload and background EMG in people with incomplete SCI. The relation

between the magnitude of the H-reflex and the amount of background EMG activity was also dependent on the position in the movement cycle. In contrast, Chauhan and Part (1992) noted in a conference proceeding that workload affected the degree of modulation during cycling in able-bodied individuals. Significantly more inhibition of the H-reflex was observed as workload increased from 0 to 30 and 150 watts. This is significant because it demonstrates that there might be a relationship between motoneuron pool activity and the size of the H-reflex. However, it was not reported how the workload was varied, so it is not known if the velocity of movement was kept constant during the trials. The change in the degree of inhibition might be attributed to an inhibitory effect of increasing movement velocity. The data have never been published in a full paper.

Cutaneous reflexes have been examined during cycling to a much smaller extent. Brown and Kukulka (1993) compared reflex responses during "free form" pedaling, pedaling with tonic levels of SOL and TA activation, and static positioning with tonic levels of SOL and TA activity. They observed that cutaneous reflex modulation occurred independently of background muscle activity. SOL reflex responses were largest (early suppression followed by later facilitation) during power phase and smallest during recovery phase during normal pedaling.

While responses changed during dynamic pedaling depending on position in the movement cycle, cutaneous reflexes were not modulated in a phase-dependent manner during static leg positioning (Brown & Kukulka, 1993). Brooke, McIlroy, Staines, Angerilli and Peritore (1999) reported similar findings during both passive pedaling and static positioning of the limb.

B. Mechanisms of H- and cutaneous reflex modulation

i. Introduction

The mechanisms that can influence the amplitude of H-reflex and the amplitude and sign of cutaneous reflexes can be categorized into two types by effect loci: central and peripheral (Brooke et al., 1992). A central mechanism refers to influences which come from the spinal cord (CPG) or higher structures in the brain (motor cortex, cerebellum). Peripheral mechanisms originate in the peripheral nervous system (and can act via interneurons on the spinal cord). Any type of sensory afferent discharge that may cause reflex modulation would fall into this category. Based on this categorization, an emerging concept is that the source of control of reflexes seems to depend on the type of reflex being studied.

ii. Peripheral mechanisms

As mentioned previously, the H-reflex has been shown to scale to background EMG levels (Crenna & Frigo, 1987; Verrier, 1985), but H-reflex behaviour is also highly task-dependent (Stein & Capaday, 1987). Clearly, modulation of the H-reflex is not simply a matter of homonymous muscle activity.

Afferent input from Ib fibres is thought to contribute to tuning force levels to task requirements, as well as to coordination of muscle activation during movement (e.g., preventing co-contraction) (Dietz, 1992). Studies of muscle activation under varying loads while walking have shown that there is generally an increase in the amplitude of the EMG bursts of leg extensors (including soleus) when the body is loaded. However, there are only small increases to the burst duration, and little or no effect on the step cycle timing (Stephens and Yang, 1999). The same results were found for both continuous and

intermittent loading of the body. Unloading the body during gait caused decreases in extensor bursts, as well as slight shortening of the stance phase of the step cycle (Stephans and Yang, 1999).

Yang et al. (1991) found no relation between the walking velocity of people with incomplete SCI and the degree to which their H-reflexes are modulated during gait. Spastic patients also showed significantly less antagonist activity in tibialis anterior, which was hypothesized to contribute to inhibition of the H-reflex (Boorman et al., 1992; Stewart & Brooke, 1993). When conditioning electrical stimuli were applied to common peroneal (CP) nerve (innervating TA) in spinal cord-intact participants, there was a significant reduction in the magnitude of the pre-motor soleus H-reflex (Stewart & Brooke, 1993). Hultborn, Meunier, Pierrot-Deseilligny and Shindo (1987) found a much smaller inhibitory effect, but used vibration of tibialis anterior to elicit the inhibitory response. Similarly, Edamura et al. (1991) noted that there was a high inverse correlation between activation of tibialis anterior and suppression of soleus H-reflex. However, in a later experiment, Yang and Whelan (1993) found that the removal of tibialis anterior activity had no effect on the suppression of the H-reflex during swing phase, suggesting that while TA activation varied inversely with H-reflex amplitude under normal gait conditions, TA activity was not itself the source of modulation. Thus, it does not seem likely that H-reflex modulation is caused by afference from an antagonist onto its corresponding agonist, acting via reciprocal inhibition.

Using systematic deactivation of different sensory receptor types in dogs, it was demonstrated that removal of discharge from muscle stretch receptors in the quadriceps could remove the inhibition of the stretch reflex normally seen during passive movement of

the knee joint (Misiaszek, Barclay, & Brooke, 1995). No other receptor had the same effect on H-reflex modulation, making it a strong candidate for being a major peripheral mechanism of SOL H-reflex modulation. Human experimentation in the same study suggested that modulation of the H-reflex was arising from stretch receptors in the knee extensor muscles (i.e., quadriceps) acting on the Ia afferents of the soleus.

More recently, Misiaszek and Pearson (1997) demonstrated that stretching the quadriceps in non-walking and walking cats caused modulation of H-reflex amplitude. In both cases, H-reflex suppression was greatest when quadriceps was stretched, with little or no inhibition while the quadriceps were shortening. Moreover, another group found that when the degree of quadriceps stretch and speed of movement were varied, increasing either the amount of estimated stretch or velocity of stretch was observed to increase suppression of the H-reflex (Cheng et al., 1995a). At equivalent rates of stretch (combination of size of stretch and speed of movement) the effect on gain was also equivalent. The effect of changing amounts of stretch was seen even under static conditions (0 rpm). Thus it was concluded that the primary endings of the muscle spindles were responsible, since Golgi tendon organs are sensitive to force generation (see also Cheng et al., 1998).

Misiaszek and Pearson (1997) noted that when EMG levels were high, a stimulus strong enough to elicit an M-wave produced an H-reflex that was not modulated, regardless of phase. However, the same stimuli with little or no background soleus EMG produced phase-modulated H-responses. Stimuli below M-threshold showed phase-dependent modulation at both low and high levels of muscle activity. The authors hypothesized that when soleus activity is high, the motoneuron pool excitability is so great

that though afferent input is inhibited, the stimulus will still evoke a maximal response. While studying contralateral modulation, Cheng et al. (1998) found that when a static leg held a tonic contraction above 30% MVC, the rate of movement of the other leg had no significant effect on SOL H-reflex. They suggested that with increasing force demands, the descending control, and that perhaps some form of corollary discharge reduces the effects of pre-synaptic inhibition caused by movement velocity.

iii. Central mechanisms

Recently, Garrett, Kerr, and Caulfield (1999) compared walking with the knee both unrestricted and restricted with a cast. Despite the cast significantly reducing the angular displacement and velocity of the knee, H-reflex showed similar modulation patterns as to those shown previously (Capaday & Stein, 1986). Similarly, no significant correlation between knee joint position and H-reflex amplitude in soleus during the walking step cycle was found (Lavoie & Capaday, 1996). As was discussed in the peripheral mechanisms section, presynaptic inhibition from knee extensor muscles onto the soleus Ia afferents is hypothesized to be a mechanism which changes H-reflex amplitude in a phase- and task-dependent manner (Cheng et al., 1995a; Misiaszek & Pearson, 1997). The results of Garrett et al. (1999) and Lavoie and Capaday (1997) do not support such a hypothesis, but instead suggest a more central mechanism.

It is difficult to explain the differences in results of Cheng et al. (1995a, 1998), Misiaszek et al. (1995) and Misiaszek and Pearson (1997) with the results of Garrett et al. (1999). One explanation may lie in the choice of points on the M-H recruitment curve used in each experiment. The Cheng and Misiaszek groups used H-reflexes elicited at

approximately 30% M_{max}, while Garrett used H_{max} to make comparisons. The difference in the position on the M-H curve may also partially explain the discrepancy in findings. It is not currently known whether the behaviour of the H-reflex is similar at different stimulation intensities.

Lavoie, Devanne & Capaday (1997) found evidence that task-dependent modulation of the H-reflex arises from central influences. When given a task in which participants must react to a "go" signal, the strongest modulation of the H-reflex occurs within the reaction time. Thus, modulation is occurring before afference resulting from task performance could even be created, and must be a result of some sort of descending signal related to task initiation.

A recent examination of cutaneous reflexes suggests that this type of reflex is influenced more by CPG circuits than by afferent discharge (Brooke et al., 1999). Passive pedaling (presumably removing activation of a pattern generating mechanism) of the legs at 20 rpm did not produce phase-dependent modulation of the cutaneous response as it had been shown previously to do in the H-reflex (McIlroy, Collins, & Brooke, 1992). Movement induced sensory discharge failed to have an effect on cutaneous reflex amplitude, indicating that a central mechanism is responsible for controlling reflex amplitude.

DeSerres, Yang and Patrick (1995), examined possible mechanisms of phase-dependent reflex reversal using single motor unit recordings. They examined the firing patterns of individual TA motor units during walking, and found that individual motor units were active both during swing and stance phase. The motor units showed an

excitatory response to stimulation during swing phase, and an inhibited or attenuated response during stance phase. These findings suggest that there are parallel inhibitory and excitatory pathways providing input to individual motor units, with the relative input from each pathway shifting as gait progresses from swing to stance. It is not known where the specific origins of control over the parallel pathways lie, but a CPG or similar rhythm-generating mechanism in the spinal cord could be used to explain such oscillating behaviour.

Phase-dependent reflex reversals observed in cats during walking (Andersson, Forssberg, Grillner, & Lindquist, 1978; Forssberg, Grillner, & Rossignol, 1975; Forssberg, 1979) have generally been attributed to the influence of a CPG for locomotion. The same type of behaviour has also been observed in humans (Yang & Stein, 1990, Duysens et al., 1992). During fictive locomotion, phasic gain control was observed by Andersson et al. (1978). Thus, in the absence of any descending or other afferent input, cutaneous afferent volleys were being modulated. With results from human experiments, Duysens et al. (1992) suggest that phase-dependence arises from a CPG, which opens and closes various peripheral pathways when their input is appropriate to modulate cutaneous reflexes during a specific phase of the movement cycle. During cycling, reflex reversals have also been reported by Brown and Kukulka (1993). These findings are also consistent with those of DeSerres et al. (1995), which also indicated that cutaneous reflexes are changed by some form of CPG.

In summary, several mechanisms have been proposed as possible influences on H-reflex gain. Some evidence has shown that the control mechanisms arise from peripheral

sensory receptors in other muscles, while some research has pointed towards more central control. Regardless of their origin, a common feature of the proposed mechanisms is how their influence acts on the reflex pathway. Presynaptic inhibition is thought to be the cause of attenuation of the H-reflex for all of the above mentioned sources of modulation.

Brooke et al., (1999) suggest that sensory afferent discharge may exert an effect on cutaneous reflexes, but act through a pattern generator, rather than simpler interneuronal pathways. Thus, it is difficult to understand the influence of specific types of afferent discharge on cutaneous reflexes because it appears to be highly processed by central mechanisms before its effect is ultimately reflected in reflex gain control.

V. Experiments

A. Rationale for the experiments

In recent years, there have been many studies examining the modulation of the H-reflex during cycling. As discussed above, there are several theories pertaining to the mechanisms which may be at least partially responsible for the observed changes of the amplitude of the soleus H-reflex with different types of movement. Discharge from velocity-sensitive stretch receptors in heteronymous and contralateral muscles have been suggested as a possible influence (Brooke et al., 1992, 1997; Cheng et al., 1995a, 1998; McIlroy et al., 1992; Misiaszek et al., 1995). Other experimental results indicate that a more central influence is responsible for H-reflex behaviour during rhythmic movement (Capaday & Stein, 1986, 1987; Lavoie & Capaday, 1996; Lavoie et al., 1997; Yang & Stein, 1990). However, there has only been limited investigation into the effects of muscle activity on H-reflex modulation during cyclic movement (Boorman et al., 1992).

Evidence from static comparisons of background EMG levels indicate that the H-reflex

should scale with background muscle activity (Crenna & Frigo, 1987; Verrier, 1985). Experiment 1 examined the possibility of activity-dependent modulation of soleus H-reflex during rhythmic cycling. If only the velocity of movement has an impact on modulation, then the direction of modulation (suppression, facilitation) should not change between workloads. If however, the muscle activity levels have bearing on modulation of the reflex, then changes in the reflex size should be observed with changes in workload.

There is evidence to show that both central and peripheral influences might act to modulate the H-reflex. It may be suggested that cutaneous reflexes seem to be controlled by central influences. In order to make a comparison between these two types of reflexes, it is necessary to compare moving trials (where a supposed CPG could be active and where afferent input is dynamically changing) to static control trials (where these influences would be tonic or not present).

Previous research on task-dependent modulation during rhythmic movement has been complicated by the phase-dependent modulation within the movement cycle. Due to the nature of rhythmic movement, joint angle, muscle activation level, and muscle stretch velocity all change phasically over the movement cycle. All of these factors have been shown previously to affect the reflex size, particularly in the H-reflex. It would be very difficult to estimate and remove the effects of each of these factors post-hoc. In these experiments, we simplified by looking at only one position of the movement cycle so factors that change throughout the phase cycle are constant across all between-task (static/dynamic contraction) comparisons.

Cutaneous and H-reflexes in soleus show some similarities in that they are phase- and task- modulated. For example, under certain circumstances, both types of reflexes can

be of greatest magnitude while the muscle is contracting. It is not yet known how they behave under varying conditions of voluntary muscle activity during rhythmic movement. An emerging concept is that while these reflexes may share similar features, the nature of the modulation they undergo may be quite different. Thus, both types of reflexes were elicited under the same conditions to compare their performance under different conditions. If the reflexes behave similarly, it might point to some common mechanism for controlling reflexes.

B. Methods

All methods and procedures were approved by the Faculty of Physical Education and Recreation Research Ethics Committee.

Twelve adult volunteers were recruited from the university community. All participants were healthy and free of any known neuromuscular disease. Due to the physically challenging nature of some of the experimental procedures, all participants completed a Physical Activity Readiness Questionnaire (PAR-Q) form in addition to signing an informed consent sheet. All procedures were explained to the participants and they were informed that they were free to withdraw from the study at any time without penalty.

Experiments 1 and 2 were typically collected concurrently and thus all of the volunteers participated in both experiments. One subject was not able to complete the entire H-reflex experiment. Their data were excluded from study in experiment 1.

C. Experiment 1: Effect of muscle activity on H-reflex modulation during leg cycling

The purpose of this set of experiments was to determine the effect of varying levels of muscle activity on the behaviour of the SOL H-reflex. In addition, static and moving conditions of matched background EMG and joint position were compared to look at possible task-dependent effects.

i. Procedures

Electromyography (EMG) was collected from the ipsilateral medial gastrocnemius (MG), SOL, TA, vastus lateralis (VL), and biceps femoris (BF) of the leg and flexor carpi radialis (FCR) of the forearm. EMG was also collected from contralateral SOL and VL. Participants were prepared for the experiment by cleaning sites over selected muscles with rubbing alcohol towelettes, then applying Ag-AgCl surface electrodes (Kendall-LTP, Chicopee, MA). Individual ground electrodes were placed over bony landmarks near each muscle. To minimize movement at the ankle, an ankle-foot orthosis was worn on the right foot. The stimulating electrodes were placed in bipolar arrangement over the tibial nerve, on the back of the right leg just above the crease in the knee. In some cases, it was necessary to arrange the electrodes such that one was placed over the tibial nerve and the other was located over the patella. A neoprene knee brace was used to wrap the stimulating electrodes to hold them in place. The leg was wrapped in tensor bandages to hold lead wires in place and reduce movement artifact. Participants wore a small pack around their waist that held the cables from the EMG channels, so as not to impede normal pedaling movement and also to reduce movement artifact. The seat height on the

cycle ergometer was adjusted so that it was a high as possible with the participant still able to pedal comfortably. The Monark cycle ergometer was modified so that cycle marker and potentiometer data could be collected to complement EMG data.

Participants pedaled the ergometer at two workloads determined by gender and body weight; these workloads corresponded approximately to loads requiring low (0.25-0.75 kp) and heavy effort (2.5-3.25 kp). Participants pedaled at a constant cadence of 60 rpm, which was self-monitored using a computer mounted on the handlebars of the ergometer. No participant had difficulty in maintaining a constant cadence. Continuous sampling of the full cycle was collected for each workload. Data were collected in each of the following conditions: a) stimulation when the ipsilateral leg was at 90° (see Figure 8-position corresponding to the "3 o'clock position") while pedaling, and b) stimulation during static contraction held at 90° with either low or high muscle activity (SOL).

During static contraction trials, the pedal was placed on wooden blocks to hold it in the 90° position, without the participant having to stabilize the body by contracting other muscles. To obtain a similar range of EMG levels as seen during cycling, subjects were told to use a strategy during the static trials. During static plantar flexion trials, participants were instructed to "push down on the pedal like they were pressing the accelerator in a car". During focused knee extension trials, participants were instructed to try to straighten their leg while still pushing down on the pedal. Participants were given visual feedback by means of an oscilloscope monitoring SOL and TA activity.

The 90° position was chosen for three reasons. At this particular position the leg extensors are the most active, making it the easiest position to observe changes in muscle activity with changing workload. Secondly, the 90° position is the point in the cycle at

which the least amount of reflex depression is observed, thus avoiding possible floor effects. Thirdly, it was possible to elicit an M-H curve at that position. In other positions, the relative position of the thigh and shank meant that the electrodes in the popliteal fossa shifted as the two segments were pressed together. The movement of the electrodes made it difficult to reliably elicit reflexes without the stimulation being painful to the participants. Maximum Voluntary Contractions (MVC) were collected for static plantar and dorsi flexion, and knee static flexion and extension, so that it was possible to normalize muscle activation levels across subjects in order to compare values. Similarly to the static experimental and control trials, the pedal was held in the proper position with wooden blocks.

One hundred sweeps were collected in each condition, with the stimulus intensity being varied so that a whole M-H response curve could be plotted. Thus in each condition, both M and H_{max} were collected. To ensure that M_{max} was reached, stimulus intensity was increased until the H-reflex was abolished and the M wave failed to get any larger when monitored on an oscilloscope.

Each sweep was initiated 40 ms pre-stimulus and lasted 100 ms, at a sampling frequency of 2000 Hz. The stimulus was a 0.5 ms square wave pulse, delivered to the right tibial nerve at 90° on every third pedal stroke of the right leg (1 stimuli approximately every 3 seconds). The stimuli were delivered automatically by the computer, which sampled a potentiometer hooked up to the right crankarm of the ergometer. Participants were instructed to maintain the same head, neck and torso orientation while data was being collected, since head and neck position has been shown

to affect the H-reflex in the lower leg (Hugon, 1973). During moving conditions, participants pedaled for bouts of approximately 5 minutes while data was collected, with brief rests periods in between trials. During static trials, participants held contractions for a minute at a time (25-30 sweeps) then were allowed to rest for a few minutes in order to avoid fatigue effects. Stimuli were delivered manually during static trials, approximately every 3-4 seconds. A fan was placed in front of the participant to keep them cool throughout the experiment, and participants were encouraged to drink water regularly during the experimental session.

ii. Data reduction

Electromyographic signals from each muscle were amplified (500-5000 X) using Grass P-511 amplifiers and band-pass filtered at 30-300Hz. Data from each EMG channel and the potentiometer were digitized using an A/D interface, sampled at a rate of 2000Hz (using Labview data acquisition software) , then stored on an IBM/PC compatible microcomputer.

A custom-designed computer program was used to process the raw data. Each EMG channel was rectified and stimulus artifact removed. The latency and peak to peak amplitude for M and H of the unrectified EMG for soleus, as well as the mean and standard deviation of the prestimulus level of activity of each channel were calculated. These values were used for further calculations.

iii. Analysis

Background muscle activity from twelve subjects was quantified by averaging the mean EMG level over a 150 msec post-stimulus period for each sweep of control trials. The sweeps were then each normalized to MVC and averaged. Often, average

background EMG is calculated using the pre-stimulus time period. Our method of calculating background EMG was used because it accurately reflects background EMG at the time when both H- and cutaneous reflexes are occurring. Using average pre-stimulus EMG only reflects a small time period prior to reflex onset, when dynamic changes in background muscle activity can occur, especially during cycling. Background muscle activity data presented in the following results section were collected during experiment 2 (cutaneous reflexes), but since the same subjects and conditions were used, it is valid to use the results for interpretation of both experiments.

Additional data were collected from six participants in order to make comparisons of H-reflex behaviour across movement type and muscle activity conditions with differing M-wave sizes. M-H curves were generated in each condition. Analyses were performed on three sizes of H-reflex: a) 30% of M_{max}, b) H_{max} and c) H that occurred at halfway (50%) of the descending limb of the M-H curve. These points of the M-H curve were chosen based on H sizes used previously (Brooke et al., 1992, Capaday & Stein, 1987, Cheng et al., 1995, Garrett et al., 1999). M_{max} was calculated by averaging the five highest peak-to-peak M waves.

In order to have consistent M-wave size within a type of analysis, M-H pairs were chosen by using the specific criteria for each type (e.g., H 30% of M_{max}) on the low muscle activitation cycling condition, then choosing M-H pairs with corresponding M-size in the other conditions. Eight to ten M-H pairs were taken from eleven participants in each condition to find an average. These three M-wave sizes were compared to see if there were any differences in the behaviour of the H-reflex with changing background levels at different points on the M-H curve. The H-reflex size has been shown previously to be

changed with conditioning electrical stimulation (Crone, Hultborn & Jesperson, 1985; Crone, Hultborn, Mazieres, Morin, Nielsen & Pierrot-Deseilligny, 1990), but the absolute size of the H-reflex response was dependent on the intensity of the test stimulus (Crone et al., 1990). What was not known was how the H-reflex would behave if conditioned with differing levels of background muscle activity. Since no difference in behaviour of the reflex across the M-sizes was found (see Results), twenty to thirty sweeps of consistent M-wave size (on the ascending limb of the M-H curve) were averaged for further analyses. Background muscle activity was calculated from the data corresponding to the selected M size.

Background muscle activity and peak to peak M and H amplitude comparisons were made using a 2 movement (moving, static) x 2 contraction level (low, high) repeated measures analysis of variance (RM ANOVA). Comparisons of H –reflex behaviour at different points on the M-H curve were completed using a 3 point of the M-H curve (H 30% of M_{max}, H_{max} and M 50% along decscending limb of M-H curve) x 2 movement (moving, static) x 2 contraction level (low, high) RM ANOVA.

iv. Results and Discussion

a. Background Muscle Activity

MG

A significant main effect for required background activity level was found ($F(1,11) = 6.015$, $p < 0.05$) ($mean_{low}$ = 103% of MVC, $mean_{high}$ = 152% of MVC). Thus, subjects were able to differentiate between high and low levels of muscle activity both during moving and static trials (see Figure 9).

SOL

Just as was observed in MG, participants had lower levels of SOL activity in the low conditions than in the high conditions ($F(1, 11) = 12.166$, $p < 0.01$) ($mean_{low}$ = 26.3% of MVC, $mean_{high}$ = 52.9% of MVC). There were no other significant effects. However, the movement type x activation level interaction approached significance (p = 0.054). While participants were able to produce low and high levels of activation while moving against a load, it was far more difficult to reproduce the activation levels during an isometric contraction (see Figure 9).

TA

There were no significant differences in the level of TA activation across conditions. However, TA activity was lower during low than high conditions ($mean_{low}$ = 0.149, $mean_{high}$ = 0.329).

VL

There was a significant main effect of required muscle activation level, with EMG amplitude being smaller during low levels of contraction(26.2% of MVC) ($F(1, 11) =$ 12.089, $p < 0.01$) than high levels of contraction (48.5% of MVC) (see Figure 9).

BF

Biceps femoris activation levels revealed a significant main effect for both movement type ($F(1, 11) = 14.938$, $p < 0.01$) and activation level ($F(1, 11) = 10.377$, $p < 0.01$). The level of activation was higher on average when activation requirements were high ($mean_{low}$ = 0.365, $mean_{high}$ = 0.655). It was also significantly higher overall during moving conditions than during static conditions ($mean_{moving}$= 0.7215, $mean_{static}$= 0.2975). The interaction between the two variables was not significant. Once again, the

subjects had difficulty matching static levels of activation to the previous levels of activity during dynamic pedaling.

FCR

Flexor carpi radialis activation levels did not vary significantly across conditions ($p > 0.1$). Thus, possible potentiation of the H-reflex via the Jendrassik maneouver is not a factor in interpreting our H-reflex results.

In summary, all leg extensor muscles were significantly different between low and high workloads, and while there was a movement type effect in BF, it is likely an artifact of the poor overall activation of this muscle (see discussion). Thus, it is likely valid to make comparisons of peak-to-peak H-reflex amplitudes across conditions.

b. M-wave and H-reflex amplitude

Mean peak-to-peak M-wave amplitude did not differ significantly across conditions (*mean*= 14.5 % ± 7 % M_{max}, see Figure 10). It can be assumed that the intensity of stimulation was consistent across all conditions, and it is possible to make comparisons of H-reflex amplitudes between conditions.

The magnitude of the peak-to-peak H-reflex was significantly smaller during low levels of muscle activation ($mean_{low}$ = 31.3% of M_{max}) than during high levels of contraction ($mean_{high}$=40.2% of M_{max})(F (1, 10) = 6.29, $p < 0.05$). There was no difference in H-reflex size between moving and static conditions (Figure 10). Hence, there was no task-dependent modulation of the H-reflex. These findings are consistent with those of Simonsen and Dyhre-Poulsen (1999).

In the present set of experiments, the pedaling cadence and joint position at which stimuli were delivered was kept constant so that the velocity of muscle shortening would

be consistent across conditions. The underlying assumption was that the input from the Ia afferents was similar in all conditions because of the control of movement velocity and joint angle. In previous cat experiments Misiaszek et al. (1995) reported Ia input from VL to be the only source of afference that caused soleus H-reflex modulation associated with cyclical movement of the limb in dogs. However, we observed modulation of the reflex with a presumed tonic level of Ia input. Clearly, while there is a wealth of evidence to show that Ia input from other muscles is a strong modulator of the H-reflex pathway (e.g., Cheng et al., 1995; Misiaszek et al., 1995, Misiaszek & Pearson, 1997), it is not the only source of modulation, since we still observed modulation when this source of input was held constant. One possibility is that the H-reflex is graded simply by the background level of excitation of the motoneuronal pool. As the level of excitability increases, the amplitude of the H-reflex increases. Another possibility is that input from force-sensitive receptors like Ib (from golgi-tendon organs) from homonymous muscles excitatory synapses onto interneuronal networks that have excitatory synapses onto the Ia terminals (or alternatively, act to inhibit an inhibitory network). An increase in muscle activation would lead to increased golgi tendon organ firing, which would in turn cause increased Ib discharge onto a network. Whether Ib input causes increased excitation or decreased inhibition, the result would be a larger reflex amplitude. The results indicate an influence of a peripheral locus for H-reflex control.

Perhaps our results can help explain the previous results of Garrett et al. (1999). They found that when joint afferent information was reduced (by bracing the knee) phase-dependent modulation of the H-reflex was not significantly changed. In our experiment, velocity-sensitive sensory afference was presumably held constant, but we still observed

changes in H-reflex amplitude with increasing background muscle activity. Under normal circumstances, it may be that both velocity- and load- sensitive afferent input act to modulate the H-reflex. In the absence of one source of information, the other source may be sufficient to control the reflex, at least to a certain extent.

H-reflexes were larger during high levels of background activation than during lower levels of background muscle activity. Cheng et al., (1998) reported that contralateral inhibition of the H-reflex during leg cycling was not seen when the stimulated leg held a strong contraction. They suggested that a factor such as Renshaw inhibition may act to disinhibit pathways that normally exert a suppressive effect on the H-reflex. It is tenable that these reflexes are meant to make contributions to force production as force requirements increase (Yang, Stein & James, 1991).

Previously, Capaday and Stein (1986, 1987) showed that there were significant differences in H-reflex size when comparing tasks like standing and walking. They observed that the H-reflex amplitude was larger at a given level of EMG during standing than during walking (and larger while walking than running). They attribute this difference to central mechanisms causing an increase in presynaptic inhibition to the Ia afferents. However, Capaday and Stein (1986, 1987) matched EMG levels between tasks without considering phase-dependent changes in reflex amplitude. Since walking has lower muscle activation requirements than running, in order to match levels of background EMG, it is necessary to compare points of highest muscle activation during walking (e.g., stance phase for SOL) with levels of lower activation during running (e.g., swing phase for SOL). In our experiments, only one phase of movement was considered, with varying levels of background activity.

How can we resolve the differences in our findings to those of Capaday and Stein (1986, 1987)? One plausible possibility is that some sort of central rhythm generator contributes to phase-dependent modulation of the H-reflex. Since the tasks have inherently different force requirements, in order to make comparisons of walking and running at a given level of EMG, it would be necessary to take data from running when SOL is least active (swing phase) and compare it to data from stance phase (SOL most active) of walking. The difference in phase would account for the differences that Capaday and Stein observed between tasks at the same level of EMG (1986, 1987), since phase-dependent modulation of the H-reflex was clearly demonstrated in the same experiments. In our experiment, phase-dependence was not an issue since only one phase was examined. Thus, the only differences we observed were between low and high levels of muscle activation, and not between static and dynamic tasks. In other words, the differences that Capaday and Stein (1987) attribute to task-dependent reflex modulation are possibly the result of phase-dependent reflex changes.

Another argument is that when Capaday and Stein calculated regression lines for different activities, they included some points during the beginning of swing phase with very low (near 0) levels of activity in SOL. These data points would change the slope of the regression line to fit through the origin and would cause the resultant regression lines to artificically appear to have different slopes (Ferris, Aagard, Simonsen, Farley & Dyhre-Poulsen, 1999). The results of Ferris et al. (1999) suggest that changing modes of locomotion does not affect the gain of the H-reflex (reflected in the slope of the H-reflex amplitude versus background EMG graph), but it does have a significant effect on the H-reflex threshold (y-intercept). Thus, when changing modes of locomotion, the size of the

H-reflex will change because of the threshold, not the reflex gain. We did not examine the effect of differing task on H-reflex threshold. However, the difference in threshold suggested that there were task-dependent differences between walking and running (Ferris et al., 1999) that was not observed between cycling and static contractions in our experiments.

c. Comparison of different points on the M-H curve

Peak-to-peak M-wave amplitude was significantly larger at the 50% point of the descending limb(*mean*= 64.7 % M_{max}) than at 30% M_{max} (*mean*= 20.3 % M_{max}) and H_{max}(M = 22.1 % M_{max}) ($F(2, 10) = 120.11$, $p = 0.000$). The peak-to-peak amplitude of the H-reflex was significantly smaller in the M 50% condition (*mean*= 21.4 % M_{max}) than both H_{max} (M= 30.8% %M_{max}) and H 30% conditions (*mean*= 29.0 % M_{max}) ($F(2, 10) = 13.518$, $p = 0.001$). However, neither the M-wave nor H-reflex showed any significant differences across movement conditions or contraction level when comparing different points on the M-H curve. It appears then that the position on the M-H curve is not a confounding variable in the interpretation of the behaviour of the H-reflex, since there was generally the same reflex behaviour at each position on the curve. The pattern of modulation was the same regardless of the reflex size, so the size of the stimulus input does not change the reflex behaviour (Figure 11). This observation is consistent with previous literature that indicates that absolute size of the H-reflex depends on the stimulus intensity, but that relative H-reflex behaviour is constant with conditioning stimulation (Crone et al., 1990).

The absence of a difference in reflex behaviour across levels of stimulation

intensity has large methodological impact. It has been established that reflex size changes with increasing stimulus intensity (Angel & Hoffmann, 1963), and it was known the behaviour of the reflex was different at various stimulus intensities (Crone et al., 1985). What was not known was whether there would be an interaction between stimulus intensity and background muscle activity. Our results show that while the absolute size of the reflex was different at different points on the M-H curve, the muscle activity-dependent modulation of the H-reflex was the same. It is then possible to make inferences using results found at different points of the M-H curve without the position on the curve being a spurious variable. This provides support for the direct comparison of data from other laboratories (i.e., Cheng et al., 1995a.; Garrett et al., 1999), but also begs the question of why these groups have differing results.

v. Summary

In experiment 1, several interesting results were revealed. From a methodological perspective, it is important to discover that the pattern of H-reflex modulation does not change depending on the intensity of the stimulus input. Thus, it is valid to compare previous experiments which have used differing M-wave sizes as controls.

When phase-dependent H-reflex modulation was controlled in this experiment by only sampling at one phase in the movement, no task-dependent modulation of the H-reflex was observed. With phase-dependence of the reflex amplitude eliminated, it was possible to see that the H-reflex amplitude increased with increased background muscle activity, independent of the type of contraction (static or dynamic). In experiment 2, we

examined cutaneous reflexes of the lower leg, to see if they behaved in the same way that H-reflexes did in the present experiment.

D. Experiment 2: Effect of muscle activation level on cutaneous reflexes during leg cycling

The purpose of this set of experiments was to examine the effect of changing background muscle activity on cutaneous reflexes of the lower leg. In addition, possible task-dependent changes in reflex behaviour were compared between moving cycling trials and matched static muscle activation at a fixed leg orientation. Combined with the information gathered in experiment 1, it is possible to make comparisons of H- and cutaneous reflex behaviour, during the same tasks and in the same participants.

i. Procedures

All experimental procedures were the same as in Experiment 1, except for details listed below. Activity of the same selected muscles, with the addition of flexor digitorum brevis (FDB) of the foot was collected using surface EMG. Stimulation was delivered via the distal tibial nerve at the ankle (near the medial malleolus) as a train of 5 x 1.0 ms pulses at 300 Hz. Stimulation intensity was constant throughout the experiment at two times radiating threshold (2 x RT), where RT is defined as the lowest intensity of stimulation at which participants felt the stimulus radiating down the foot towards the toes. A stimulus was delivered when the right leg reached 90° on every third cycle. Thirty sweeps were collected in each condition, including a 1) control, no-stimulation condition, 2) a moving stimulated condition, as well as 3) static trials of both focused a) plantar flexion and b) knee extension. All moving and static conditions were performed at the same two loads

(low and high) as in Experiment 1. The MVC data from experiment 1 was used to normalize muscle activity for both experiments.

ii. Data reduction and analysis

Just as in Experiment 1, electromyographic signals from each muscle were amplified (5000 x) using a pre-amplifier and band-pass filtered at 30-300Hz. Data from each channel were digitized using an A/D interface, sampled at a rate of 1000Hz, then stored on computer hard disk. Data were collected for twelve subjects in Experiment 2.

Raw data were examined using an interactive computer program. Stimulus artifact was removed and the EMG were filtered using a 21-point moving average filter. The control, unstimulated (no stimulus to the nerve) EMG traces were subtracted from the stimulated (stimulus delivered to the nerve) EMG. The resultant subtracted data was used for subsequent analysis, including $ACRE_{150}$ net reflex effects. ACRE (average cumulative reflex effect) is a measure calculated to give the net reflex effect over a given window of time (e.g., $ACRE_{150}$ represents net reflex response over 150 ms post-stimulus). It is calculated by taking EMG (with stimulus artifact removed) and integrating the EMG over a given time interval (e.g., 150 ms) then dividing the result by the time interval, and finally normalizing the net reflex to the Maximum Voluntary Contraction (MVC) of the muscle under study. A positive ACRE value represents a net facilitation, while a negative value indicates net suppression (Zehr, Fujita & Stein, 1997).

In addition to $ACRE_{150}$, the latency and magnitude of all significant phasic facilitations and suppressions of the EMG were calculated. To be considered significant, facilitation had to be greater than two standard deviations larger than the mean EMG (over 250 ms), while a significant suppression was operationalised as being greater than

two standard deviations smaller than the mean EMG. Thirty sweeps were averaged together to find the mean cutaneous reflex responses for each condition.

Significant responses were visually selected using the aforementioned rule, then put into bins post-hoc, based on their latencies of onset. The bin sizes were determined by examining a frequency distribution plot of all of the responses. The latencies early (40-65 msec) middle (70-120 msec) and late (130 msec and longer) were consistent with previous papers (Duysens et al., 1993; Yang & Stein, 1990). All responses occurring outside of the latencies were discarded.

As indicated in experiment 1, the level of background muscle activity during moving trials was determined from unperturbed trials, averaged across sweeps and normalized to MVC for analysis. Peak-to-peak M-wave size in FDB was calculated to confirm that stimulus intensity was consistent across conditions. Net reflexes and individual phasic responses were normalized to raw background EMG levels for each trial. In addition, net and phasic responses were normalized to MVC. This procedure was completed to see if reflex responses were different from each other in absolute magnitude. To determine whether the net reflex response was significantly different from normal muscle activity, $ACRE_{150}$ values were compared to background levels of muscle activity using a paired t-test for each muscle. A t-test was run for each of low and high muscle activation and moving and static conditions in each muscle (for a total of 20 separate t-tests).

To make direct comparisons between H- and cutaneous reflexes, SOL middle latency response and $ACRE_{150}$ values were normalized to M_{max} for the corresponding

condition from Experiment 1. This was only possible to do with SOL, since we only had M and H data for this muscle.

All net reflex responses, background EMG activity and M-wave amplitudes (FDB only) were all analysed using a 2 contraction level (low, high) x 2 movement type (moving, static) repeated measures ANOVA. Each muscle was analysed separately, because we were interested only in differences within a muscle.

When analyzing phasic cutaneous data, it was not possible to use a RM ANOVA, since not all of the participants exhibited a significant reflex response at each latency, particularly in the upper leg muscles. Instead, a one-way ANOVA was performed on the significant responses for early, middle and late latencies comparing the magnitudes of all significant responses in each condition. A separate ANOVA was calculated for each muscle and latency.

iii. Results and Discussion

a. Background muscle activity and M-wave size

M-wave peak-to-peak amplitude in FDB was not different across conditions ($p>0.07$). Therefore, we assume that stimulus intensity was not different across conditions. For background muscle activity, please refer to experiment 1, and Figure 9.

b. Phasic responses

Note: Degrees of freedom in the significant results will vary depending on the number of significant responses (see section D. ii) for each muscle at each response latency.

In MG, the middle latency response (70-120 ms post-stimulus) had a significant effect for the type of movement. During moving conditions, the middle response was inhibitory ($mean_{moving}$ = -6.4 % of MVC), while under static conditions it was excitatory ($mean_{static}$= 91.2 % of MVC) (F 1, 30) = 7.747, $p < 0.01$, see Figure 12) when the response was normalized to background muscle activity. The difference between moving and static conditions was still observed when normalized to MVC ($p < 0.05$). There were no differences between conditions at either the early or late latency.

Similar to the behaviour of MG responses, there was no difference in SOL response between conditions at either the early or late latency. Relative to background muscle activity, the middle latency revealed a main effect for movement type (normalized to background activity, F (1,23) = 11.516, $p < 0.01$), with very small or inhibitory responses during movement ($mean_{moving}$ = 6.3 % of MVC), and much larger excitatory responses during static conditions ($mean_{static}$= 90 % of MVC). These results were maintained relative to maximum voluntary contraction ($p < 0.01$). When SOL middle latency responses were compared when normalized to M_{max}, the same significant difference between tasks was observed. Responses were significantly smaller during movement than under static conditions ($mean_{moving}$= 0.2% M_{max}, $mean_{static}$=1.2% M_{max}).

Vastus lateralis exhibited reflex behaviour similar to MG and SOL. In this case, both early (F (1,17) = 7.656, p < 0.05) and mid (F (1, 19), p < 0.05) latency responses were either very small or inhibitory during movement ($mean_{mid}$ = 3.3 % of MVC), and larger excitatory responses during matched static contractions ($mean_{mid}$ =97.5% of MVC). However, the same significant result was not observed when the VL middle response was normalized to MVC ($p = 0.122$). Phasic responses in tibialis anterior did not exhibit any

differences in behaviour with changing levels of background activity or the type of contraction. BF showed no differences in phasic responses across conditions. The activity and phase of movement chosen did not require high activation of TA and BF, in fact the joint positioning and extensor task made it somewhat difficult to activate these muscles, particularly BF. Tibialis anterior activation ranged from only 10-25% of MVC. BF activation levels were higher relative to MVC for this joint position (very close to MVC), but still may not reflect a large proportion of BF muscle fibres being active, since it was very difficult to statically contract BF with the leg in this position. Thus, the MVC collected may not be a true maximal value. The joint angle may then prevent there being differences between conditions. At any rate, the knee flexors were not very active, but were not key muscles of interest like SOL.

Our findings are consistent with previous research that suggests that the most (and sometimes only) significant cutaneous responses occur at the middle (or P2 in animal models) latency response (Duysens et al., 1990, 1993, 1996; Tax et al., 1995; Yang & Stein, 1990). This latency has been suggested to correspond to responses generated by a polysynaptic pathway (Yang & Stein, 1990), which could include effects from a CPG network.

Phasic cutaneous responses were generally similar amongst knee and ankle extensor muscles. Overall, cutaneous responses were larger and excitatory responses during static contraction, but were much smaller and/or inhibitory during movement. Degree of muscle activation was not a factor in determining the size of the response.

The task-dependent reversal of the middle latency response in the leg extensors adds credence to the notion that cutaneous reflexes are controlled by a CPG for rhythmic

movement. Even though afferent discharge under both static and dynamic conditions should be very similar, the reflex was excitatory under static conditions and inhibitory under dynamic conditions. These results would indicate that some sort of central mechanism is at least partially responsible for the observed differences, since changes in peripheral influences like input from load receptors did not seem to exert an effect. One possibility is a gating mechanism, with differential control of reflexes arising from a switch in the type of movement. Parallel pathways of inhibitory and excitatory control could be switched on and off by a mechanism either in the spinal cord or the brain. Duysens et al. (1992) suggested such a mechanism that would rely on a central pattern generator to open and close excitatory pathways at the appropriate times during gait. A similar suggestion was made earlier by Yang and Stein (1990) with respect to observed phase-dependence of cutaneous reflex responses (see also DeSerres et al., 1995). However, our experiment did not control input to receptors sensing changes in velocity or acceleration, which have not previously been considered to be a factor in controlling reflex behaviour.

c. Net reflexes

The average cumulative reflex after 150 milliseconds ($ACRE_{150}$) normalized to background muscle activity was used as a measure of the net reflex response in each muscle (Figure 13). In MG, there was a significant effect of movement type (F (1, 11) = 7.276, $p < 0.05$). Net reflexes were inhibitory during movement ($mean_{moving}$ = -12.6 % of MVC) and excitatory during static contraction ($mean_{static}$=12.5 % of MVC). This pattern persisted when reflexes were compared normalized to MVC ($F(1,11) = 4.98$, $p < 0.05$).

The same pattern was observed in SOL, though the effect did not reach significance using either method of analysis (background muscle activity, F (1, 11) =

3.300, $p = 0.097$, MVC, $F(1, 11) = 3.57$, $p = 0.085$). Similarly, there was no significant movement type or muscle activity activity effect when SOL net response was normalized to M_{max}.

There were no significant responses for any other muscle. In general, cutaneous responses in VL and BF became larger relative to background activity during static contraction. Our results are contrary to those observed by Komiyama, Zehr & Stein (in press) who found that cutaneous reflexes of the lower leg were suppressed during standing, but were facilitated during walking.

Paired t-test comparisons of the disturbed and undisturbed EMG at 150 ms post-stimulus for each muscle revealed a significant suppression of MG activity with stimulation while moving ($p < 0.05$). Conversely, TA responses were excitatory during static contractions ($p < 0.05$). No other conditions caused a significant change in muscle activity. Again, the task-specific (moving versus static) reflex reversal indicates that control of cutaneous reflexes might be of central origin.

Net reflexes did not vary significantly across conditions. The small number of significant facilitatory and inhibitory phasic responses at all latencies translated to very small overall effects. It is not known whether the reflexes would have significantly impacted movement kinematics as they have been shown to during walking (Zehr et al., 1998), since such data was not collected. However, it would seem unlikely that joint angles would change significantly, since movement was highly constrained by the foot being attached to the pedal.

Forssberg et al. (1975) described cutaneous reflex modulation during stance phase of walking. They found the responses in the extensor muscles to be excitatory, while the

flexor muscle responses were inhibitory. Presumably, this is because the extensors are actively supporting body weight and the flexors are fairly quiet. Cutaneous reflexes have also been shown to contribute to changing gait kinematics to avoid "obstacles" (Zehr et al., 1998). It might be expected then, that since cutaneous reflexes seem to add to already present muscle activation patterns, that reflex amplitude would also scale with background muscle activity. This does not appear to be the case in our data , as cutaneous reflexes were shown to be inhibitory during the pedaling 'push' phase, which would most closely resemble stance phase of gait. Again, this observation might also be limited by saturation of the motoneuron pool that would prevent excitation from being observed. This does not seem likely, however, since participants were able to pedal for prolonged periods of time at the high workload, suggesting that they had not reached their maximal capacity. Alternatively, the differences may be due to differential control of leg cycling and gait.

The significant differences in cutaneous reflex amplitude between dynamic and static contraction indicates that cutaneous reflex behaviour is task-dependent. Previously, Evans, Harrison & Stephens (1989), demonstrated that cutaneous reflex behaviour in the finger and hand muscles was dependent on the joint positioning while isometric activity was performed. Similarly, Burke et al., (1991) observed differential reflex behaviour when the muscle was active versus silent. More recently, Komiyama, Zehr & Stein (in press) observed task-dependent behaviour of lower leg cutaneous reflexes between walking and standing (while matching ankle orientation to walking). Assuming peripheral afferent input was the same in both the static and dynamic tasks, the task-dependent behaviour is possibly arising from a central influence. The potential source of the central input cannot be determined from this experiment, but could be of either spinal or cortical origin.

However, the results Komiyama et al. (1999) observed are opposite to those we observed in our experiments (excitatory responses during walking, inhibitory responses during standing). With the high degree of similarity between the two experimental methods, the most logical explanation for the opposite results is that there are large differences in the neural control of walking versus cycling.

d. Summary

In Experiment 2, neither phasic nor net responses were affected by changes in background muscle activity. Even with significant differences in muscle activity between low and high conditions, modulation of cutaneous reflex responses did not change with changing background EMG. They were, however, significantly modulated according to task: that is they were different during dynamic contraction than during static contraction. In muscles that act as synergists during cycling (MG, SOL, VL), middle latency phasic responses were larger excitatory responses during static contraction, but small and/or inhibitory during movement.

E. General discussion

These experiments addressed several issues pertaining to reflex behaviour during rhythmic movement. First, clarification was needed as to the behaviour of the H-reflex elicited with different stimulus intensities. Previous investigations have used different criterion M-wave sizes, making comparisons of results from different papers difficult. The results of this set of experiments indicate that the selected M-wave size does not have an effect on the overall pattern of behaviour of the H-reflex, making comparisons of different previous experiments less complicated.

Secondly, while the H-reflex has been shown previously to scale with background

EMG (Capaday & Stein, 1986, 1987), the scaling seemed to be complicated by task-dependent differences in H-reflex amplitude. An advantage of using cycling as an experimental paradigm was that it was possible to examine varying levels of muscle activity while maintaining movement velocity and movement pattern as constants, which would not have been possible using walking or running. This enabled us to separate phase-dependency of the reflexes from task-dependency. Experiment 1 simplified analysis of task-dependent changes in the H-reflex, with the results indicating that background muscle activity had a significant effect on the H-reflex, independent of the mode of muscle activity (dynamic or static) during leg cycling.

Finally, a direct comparison of H- and cutaneous reflex behaviour had never been made in the same subjects using the same paradigm for both reflexes. In addition, the behaviour of cutaneous reflexes with varying levels of background muscle activity was unclear. It was not known whether the behaviour of the two types of reflexes would change in the same way across conditions, or if the control of these reflexes originated from different sources and thus their behaviour would differ.

Romano and Schieppati (1987) observed that H-reflex amplitude was highly dependent on the type of contraction being made while the reflex is elicited. During concentric (muscle shortening) contractions, H-reflex amplitude increased with increasing background EMG, while during eccentric (muscle lengthening) contractions, H-reflex decreased with increasing EMG. They concluded that the effect must arise from a presynaptic origin, since it was independent of descending drive to the muscle. The difference in reflex behaviour, they hypothesized, was to better match muscle output to the descending nervous command (since muscle mechanical properties differ depending on

the type of contraction) (Romano & Schieppati, 1987). However, implicit in matching output with input is the presence of a comparator mechanism that would be associated with a form of CPG. Our results indicate that peripheral input (from changing background muscle activation) had an effect on the resultant amplitude of the H-reflex. Thus the control of the H-reflex seems to be a complicated interaction between peripheral and central factors.

Cutaneous reflexes, on the other hand, seem to be influenced more centrally. The absence of load-dependent modulation, in addition to the observation of task-dependence in our results suggests that cutaneous reflexes are likely governed by central influences, either from the brain or spinal cord. There is ample evidence from previous work to support this idea (Brown & Kukulka, 1993; DeSerres et al., 1995; Duysens et al., 1992; Komiyama et al.,in press; Van Wezel et al., 1997; Yang & Stein, 1990). Brown & Kukulka (1993) observed phase-dependent modulation of cutaneous reflexes during cycling movements, but not during matched static positioning and activity of the lower leg muscles. Cutaneous reflexes do not seem to be affected by changes in peripheral sensory input, except in the presence of a rhythm-generating mechanism. However, a limitation of this experiment was that we were not able to control all types of afference. It is not known how differences in acceleration between the two types of activity (moving and static contraction) might have affected the results, or if they even play a role in controlling cutaneous reflex activity.

Thus, while H- and cutaneous reflexes show some similarities in behaviour under certain conditions (e.g., phase modulation), they do not appear to be controlled by the same mechanisms. Nor will their patterns of modulation always be parallel. When a

direct comparison of H- and cutaneous reflexes was made (Figure 14), H-reflexes scale to background muscle activity, while cutaneous reflex behaviour was dependent on task. During cycling, H-reflex has been shown previously to be highly sensitive to the velocity of movement (Cheng et al., 1995a; McIlroy et al., 1992), and our results also indicate a sensitivity to muscle activity levels. Cutaneous reflexes have not been shown to change with either of these variables, but do change as the mode of locomotion changes as we have observed in these experiments, as well as previously (Komiyama et al., in press). Thus, the changes in reflex response will be different as the context of movement changes for each type of reflex. Additionally, since we only made comparisons of reflexes at one point in the movement cycle, it is not known how the behaviour of H- and cutaneous reflexes would compare at other points in the cycling movement cycle.

When interpreting the implications of our results, a question that must then be considered is, are leg ergometry and walking under the same neural control? The tasks are highly similar, both requiring alternating leg movements. However, the joint kinematics are fairly different and cycling does not require bearing body weight to the same extent that walking or running does. Are these differences also reflected in differing reflex behaviour?

Clear differences in reflex behaviour have been observed between gait and cycling. H-reflexes show some differences between these tasks. The pattern of phase modulation is somewhat different between walking (Capaday & Stein, 1987) and cycling (Brooke et al, 1992). More marked differences are seen in cutaneous reflexes. Komiyama et al. (in press) observed facilitatory cutaneous reflex responses during walking (at initial heel-down of the step cycle) when compared to reflexes elicited during standing with matched

posture and joint position. During cycling, we observed the opposite effect, where reflexes were suppressed during cycling movement versus static controls.

Why are there differences in reflex behaviour between gait and cycling? While the tasks are very similar in that the legs move in opposition and the muscles are turned on and off phasically, there are significant differences between the tasks. Walking and running are weight-bearing activities, while cycling is not. Also, the kinematics of leg movement, while similar, are not the same. The answer is not known, yet differences in their central control may explain differences in the influence of peripheral input. From a methodological and theoretical perspective, it draws into question the validity of making inferences about gait from experimental evidence gained using cycling as a paradigm.

There are a few possible reasons for why H-reflexes and cutaneous reflexes behave differently. The H-reflex is a myotatic reflex, and increasing reflex response amplitude with increasing background muscle activity may be necessary because its analogue, the stretch reflex, is used to correct disturbances during gait by contributing to force production (Dietz et al., 1979; Yang, Stein & James, 1991). During cycling (at the joint position we examined), a perceived stretch of soleus muscle would indicate that more force was required to move the pedal in the forward direction. Increasing stretch reflex response with increasing background muscle activity would logically scale the reflex contribution to moving the pedal. The H-reflex (as a means of studying stretch reflex pathway behaviour) is thus highly sensitive to peripheral afferent input.

Cutaneous reflexes, on the other hand, seem to contribute more to balance and the maintenance of an upright posture (Zehr & Stein, 1999). While exhibiting a similar pattern of phase-dependent modulation as the H-reflex (Brown & Kukulka, 1993), the

maintenance of balance might also have different requirements, depending on whether the task is static or dynamic. Another explanation could be that in our task, cycling, cutaneous reflexes are not necessary since a perturbation to the sole of the foot is unlikely while pedalling. The reflexes would be down-regulated, and they would be very small compared to reflexes elicited during static postures. Based on the present results, it would appear that some central influence, whether it be some sort of basic spinal generating network, or descending signals from centres in the brain, is at least partially responsible for gating the pathways which modulate H- and cutaneous reflexes.

Methodological Considerations

One of the main methodological considerations when interpreting the results of these experiments is the difficulty in matching levels of EMG. Even with a source of visual feedback to guide their efforts, participants had great difficulty in replicating dynamic muscle activation levels during static contraction. In the future, subjects would benefit from a training period of a few practice days to get accustomed to matching SOL and TA activation levels during static contraction.

Future Directions

A direct comparison of walking and cycling seems to be necessary to answer the questions arising from this experiment. Using a paradigm similar to the one in this experiment, H- and cutaneous reflexes could be compared during different activities. Additionally, we focused on one movement phase only, where reflexes are generally facilitated. It is not known whether or not the same behavioural pattern would hold during other phases of cycling movement, particularly recovery phase, where reflexes are normally suppressed. However, we predict that the same behaviour that was observed in

the present experiments would persist.

Conclusions

In conclusion, the behaviour of H and cutaneous reflexes showed some similarities and some critical differences. H-reflex amplitude increased with increasing background muscle activity, while cutaneous reflexes tended to become smaller and/or inhibitory (though not significantly so). Of particular interest was the difference in task-specific modulation. H-reflexes were not significantly different between the static and moving trials, indicating that the similar afference produced similar H-reflex amplitudes. Cutaneous reflexes, on the other hand, were reversed when comparing static to moving conditions, in spite of very similar sensory discharge. Thus, the two types of reflexes do not seem to be under similar control. This difference is most likely related to their differing roles during locomotion.

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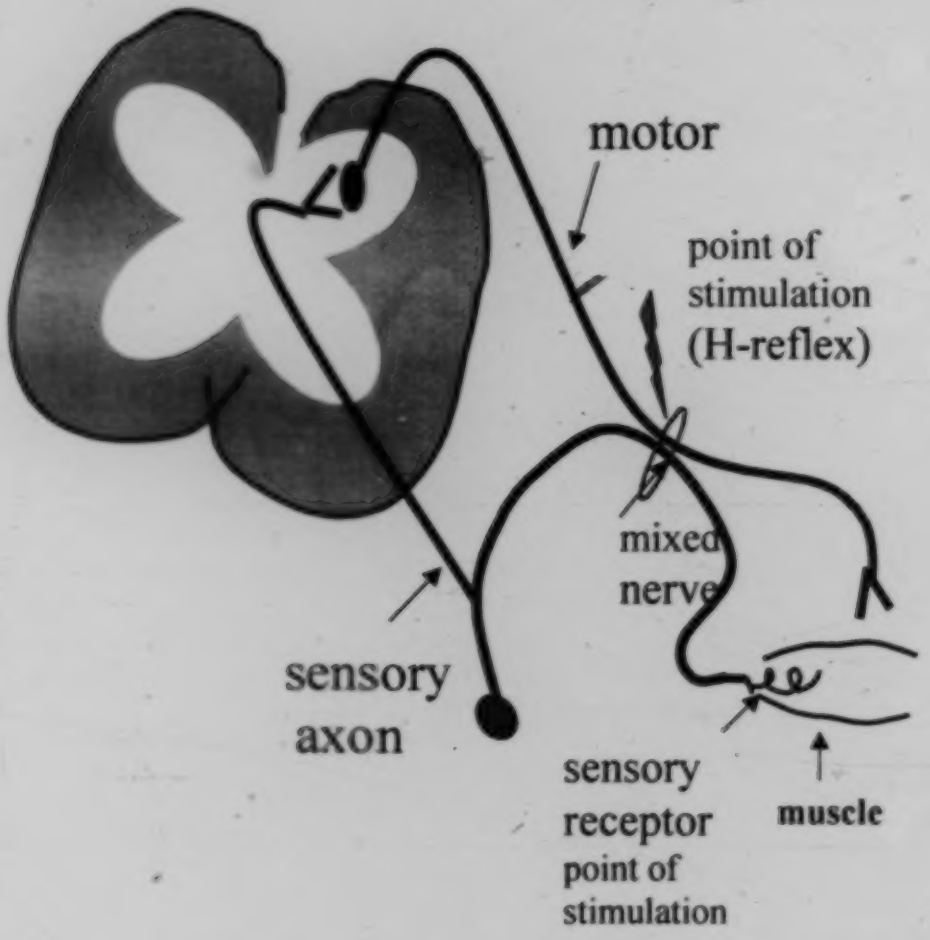
VI. Figures

Figure 1- Functional anatomy of the H- and stretch reflex pathway. The point of stimulation is typical of H-reflex experimentation. In the stretch reflex, the imposed stretch is detected by the muscle spindles and transmitted via the Ia afferent fibres.



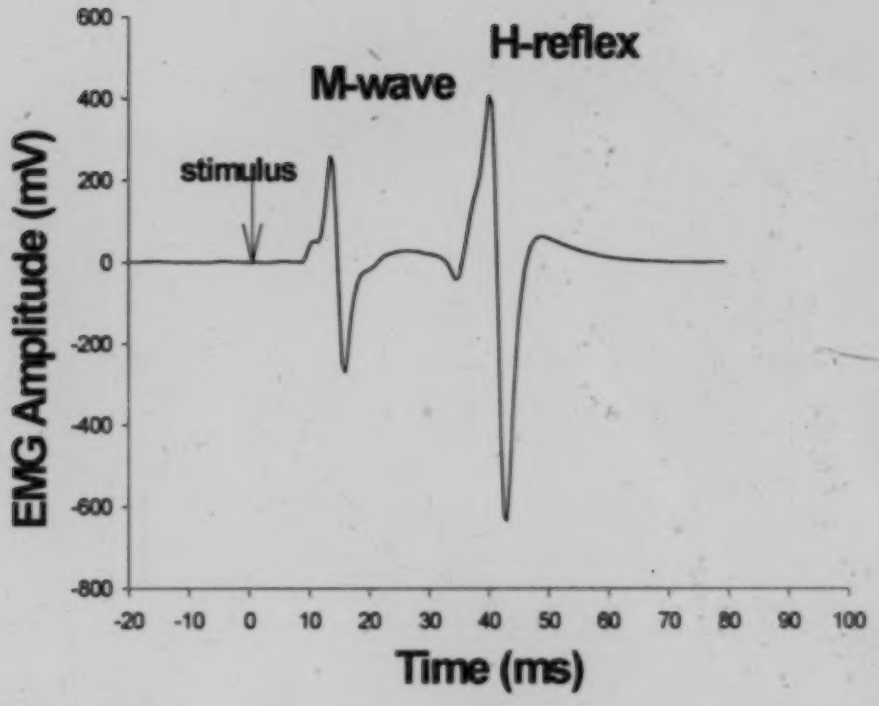


Figure 2- A typical M-H waveform profile from Soleus muscle (elicited via Tibial N) The M-wave has an approximately 5-10 msec latency and the H-reflex has an approximately 35-45 msec latency.

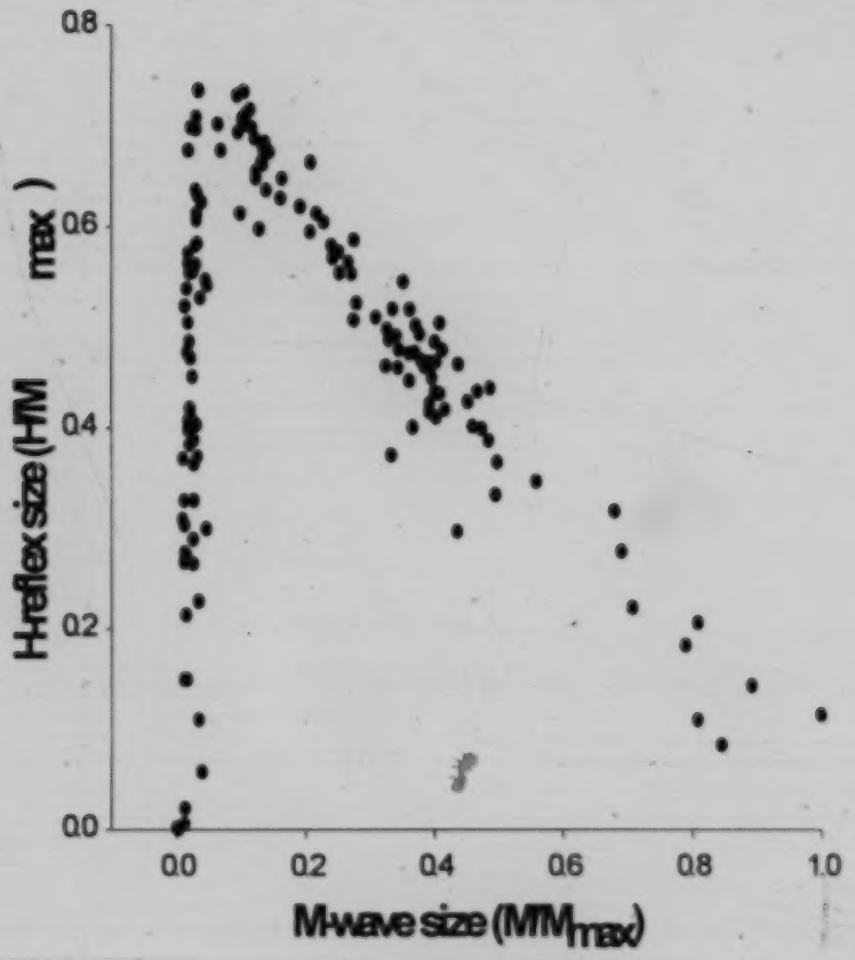


Figure 3- An M-wave- H-reflex curve. Note that the H-reflex amplitude will increase with increasing M-wave size until H_{max}, then decrease until being almost or completely abolished at M_{max}.

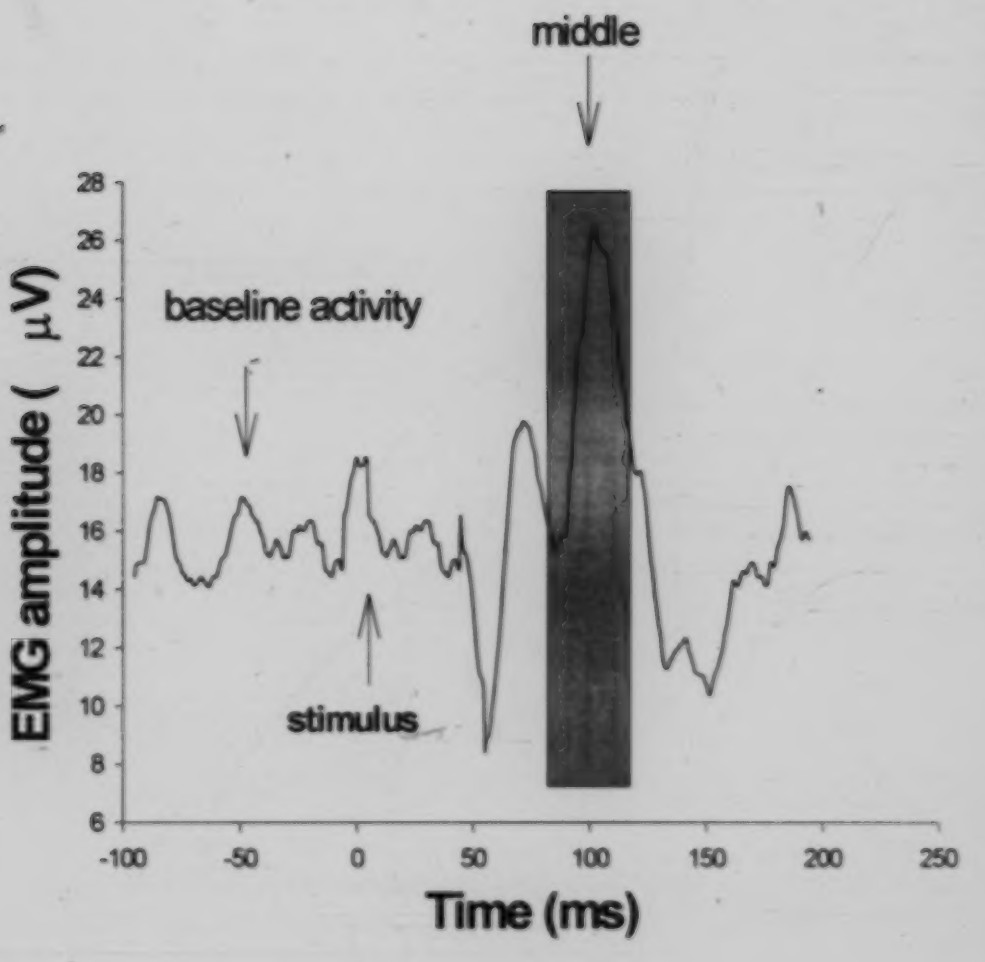
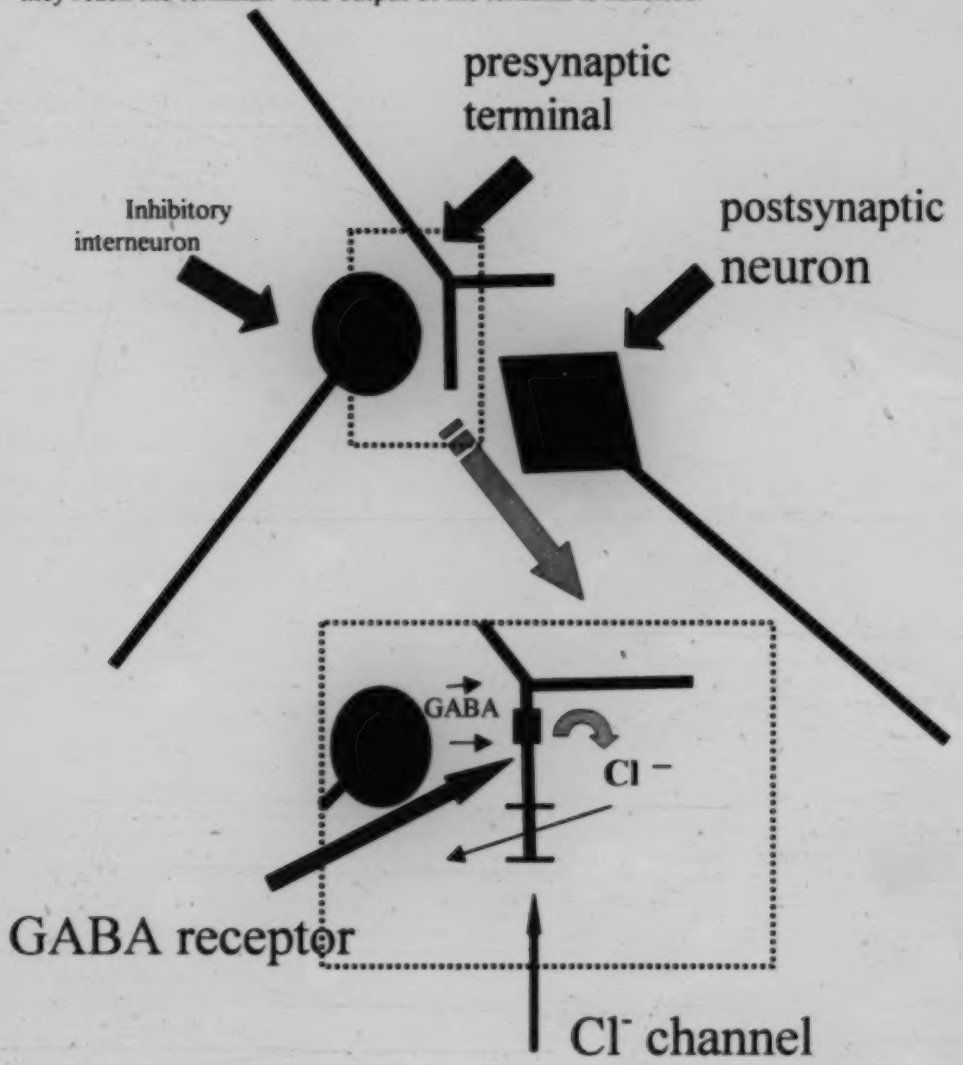


Figure 4 – Sample of a cutaneous reflex (filtered with 21-point moving average filter). Stimulation is applied at T= 0. In this example, the early and late latencies (40-65 and 130 + ms, respectively) show inhibitory responses (relative to baseline) , while the middle latency exhibits an excitatory response (see darkened area).

Figure 5- Representation of hypothesized mechanism of presynaptic inhibition and primary afferent depolarization. Chloride ions leaving the terminal depolarizes the terminal to a small extent, so that action potentials traveling down the axon have lower efficacy when they reach the terminal. The output of the terminal is inhibited.



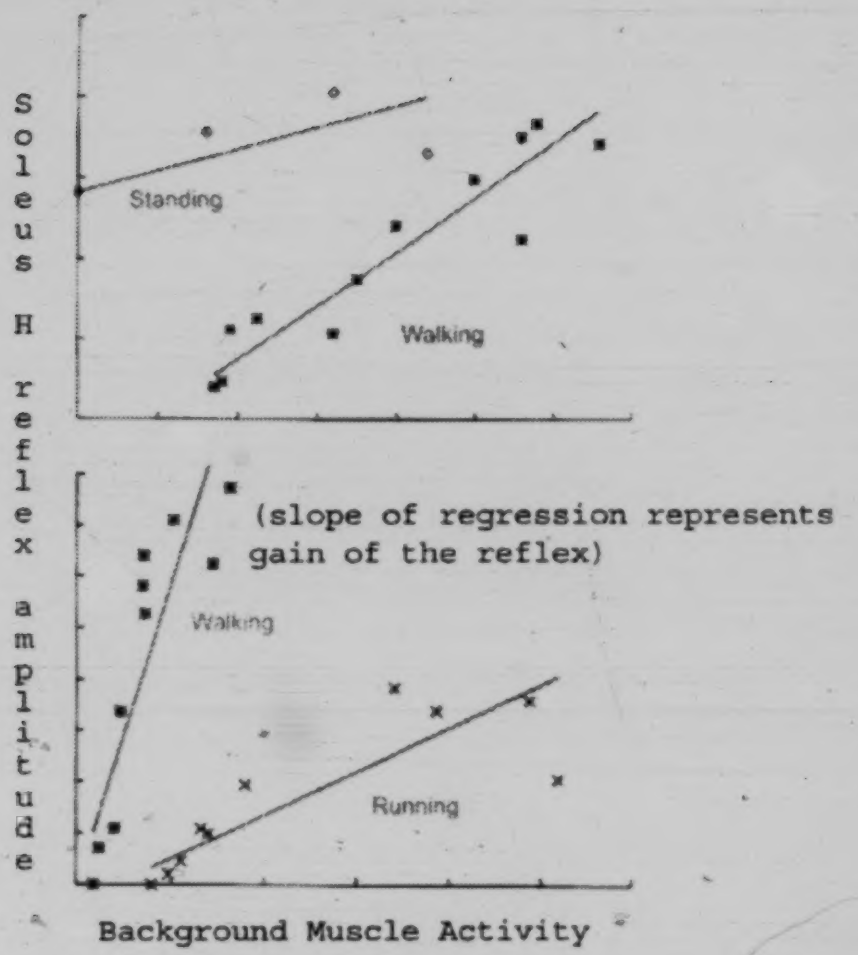
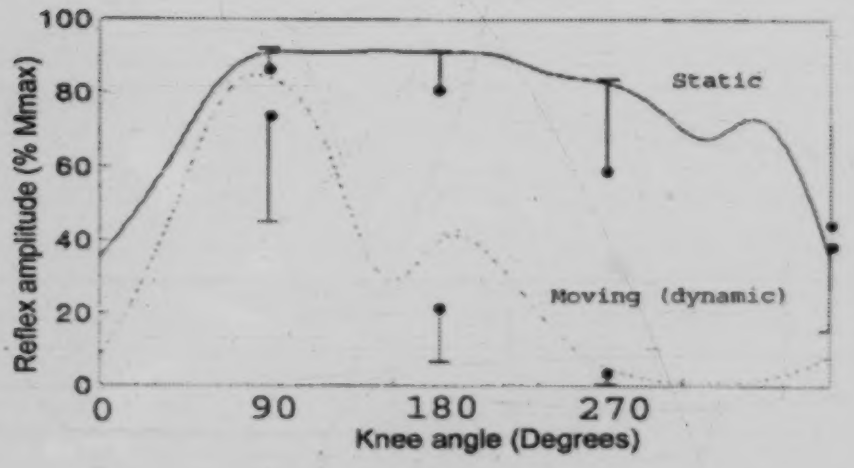


Figure 6: Soleus H-reflex amplitude vs Background Soleus muscle activity during standing, walking and running. While the amplitude of the reflex increases with increasing muscle activity in general, the gain of the H-reflex is highly task-dependent.

Figure 7- Pattern of H-reflex modulation during leg cycling (adapted from Brooke et al., 1992).



(Adapted from Brooke, McIlroy & Collins, 1992)

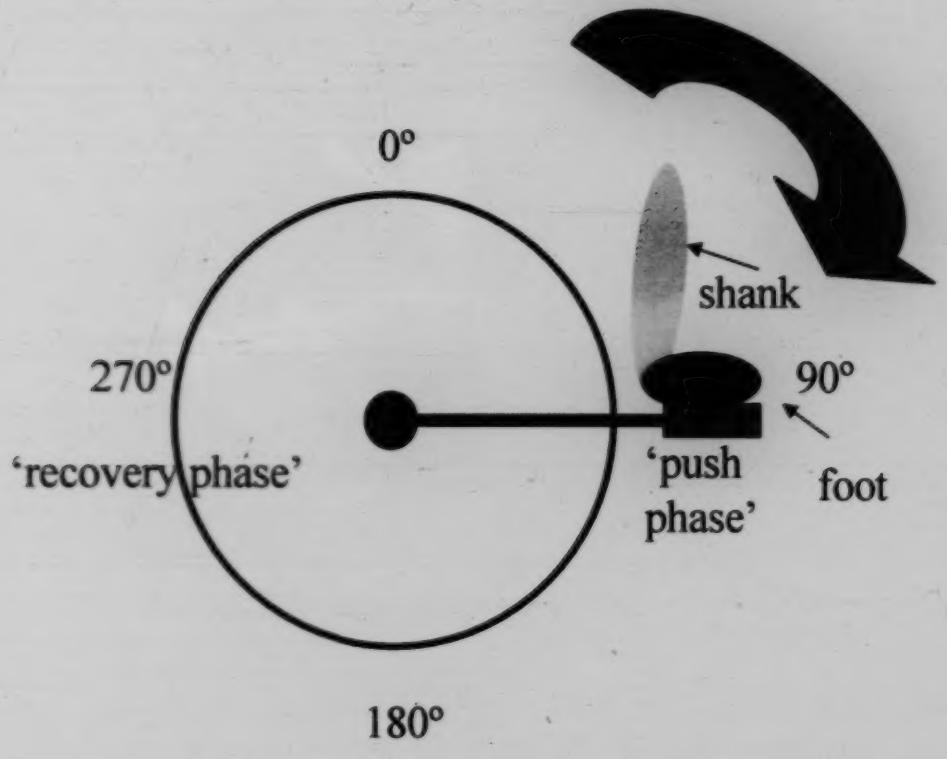


Figure 8- Representation of the pedal position at which reflexes were elicited (90°).

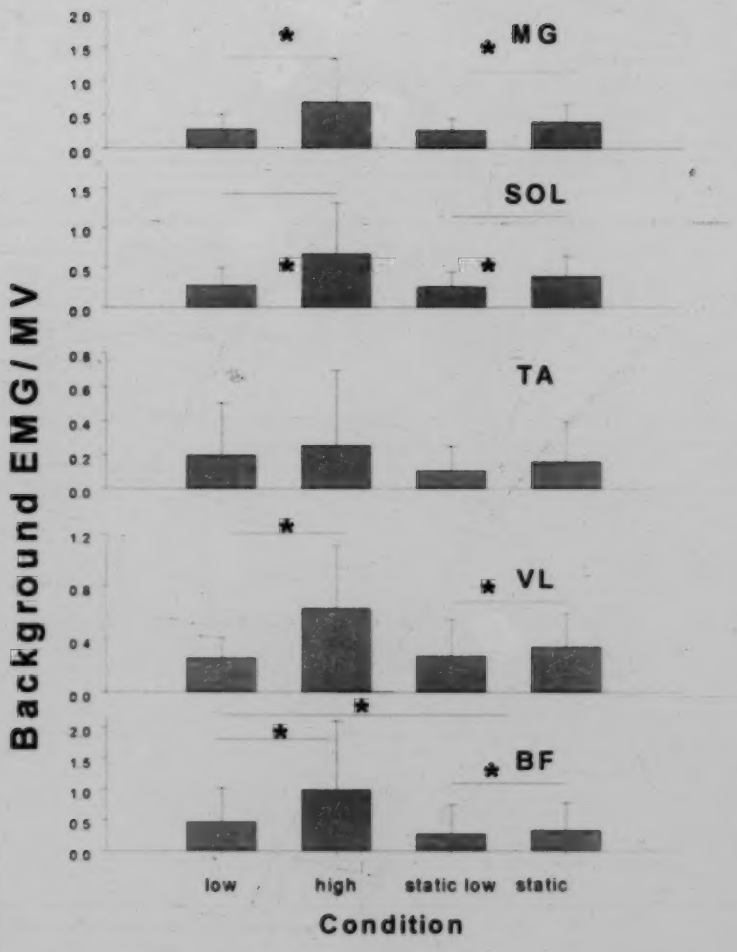


Figure 9 – Experiment 1: Background muscle activity in medial gastrocnemius (MG) soleus (SOL), tibialis anterior (TA), vastus lateralis (VL) and biceps femoris (BF) during each of the movement conditions. There is a significant difference ($p < 0.05$, indicated by *) between high and low moving and static conditions in MG, SOL , VL and BF with EMG amplitude being significantly higher during high contraction. There was also a significant effect of movement type (static, moving) observed in BF. No other differences are significant. Shown are mean values (with standard deviation).

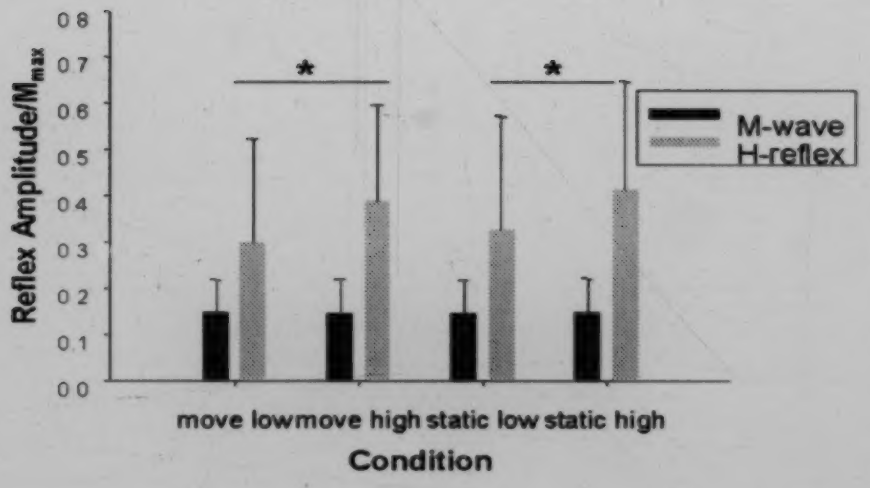


Figure 10- Experiment 1: M-wave and H-reflex amplitudes for each movement condition. M-wave amplitude did not differ significantly across conditions, while H-reflex amplitudes were significantly different between the low and high conditions. No differences existed between static and moving conditions. Shown are mean values (with standard deviation).

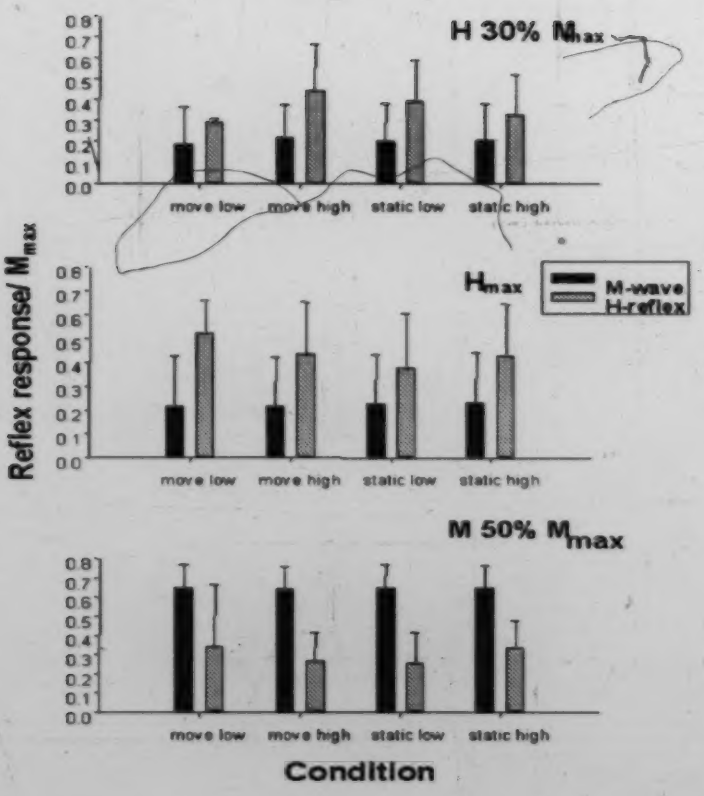


Figure 11 - Experiment 1: M-wave and H-reflex peak-to-peak amplitudes for each condition at H 30% M_{max} (top), H_{max} (middle) and M at 50% of the descending limb of the M-H curve (bottom). Though there are differences in the size of the M- and H-responses at each position, there are no significant differences in behaviour of the reflex at each level of muscle activity or movement type at different positions on the M-H curve. Mean values are shown with standard deviation.

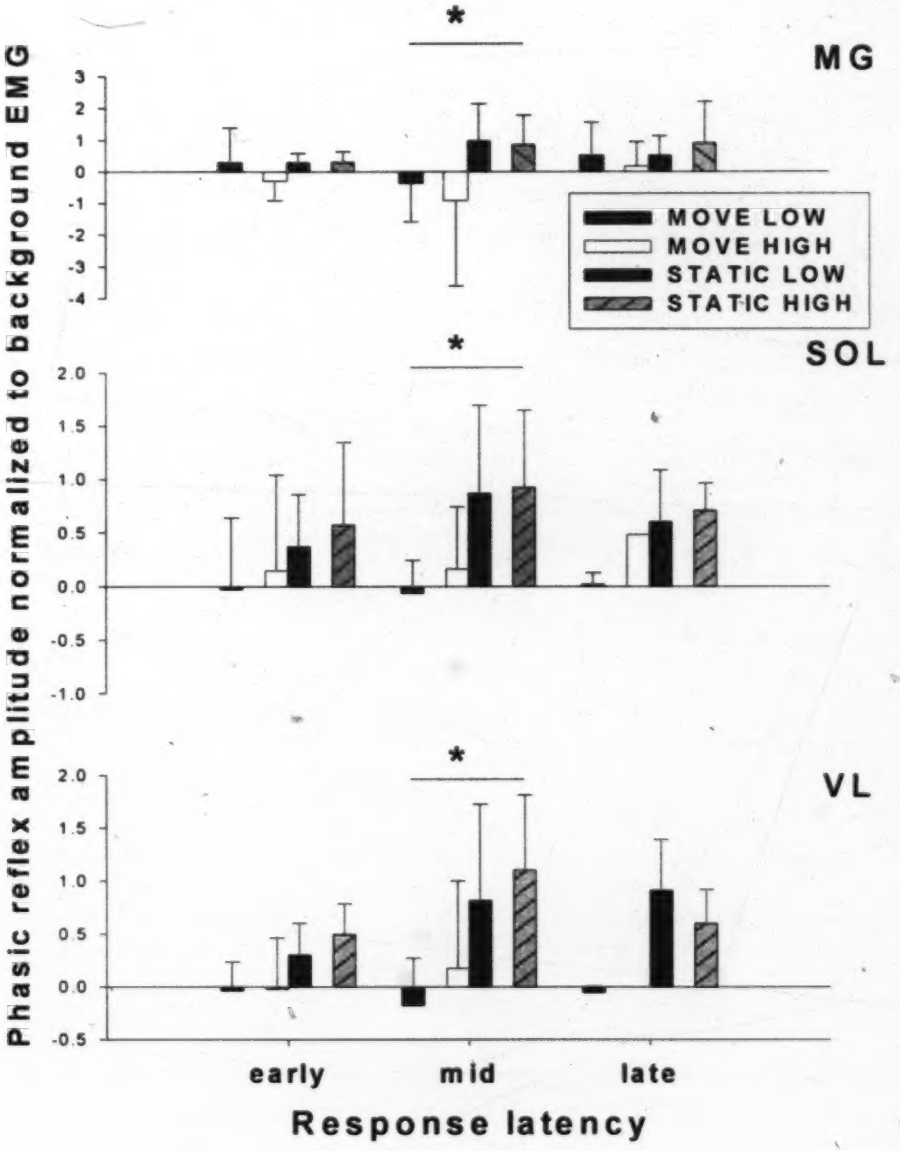


Figure 12 - Experiment 2: Phasic responses at early, middle and late latencies for each condition. During moving trials, responses are small excitatory or inhibitory responses. During static contractions, much larger excitatory responses are observed, particularly at the middle latency. Mean reflex values are displayed with standard deviation.

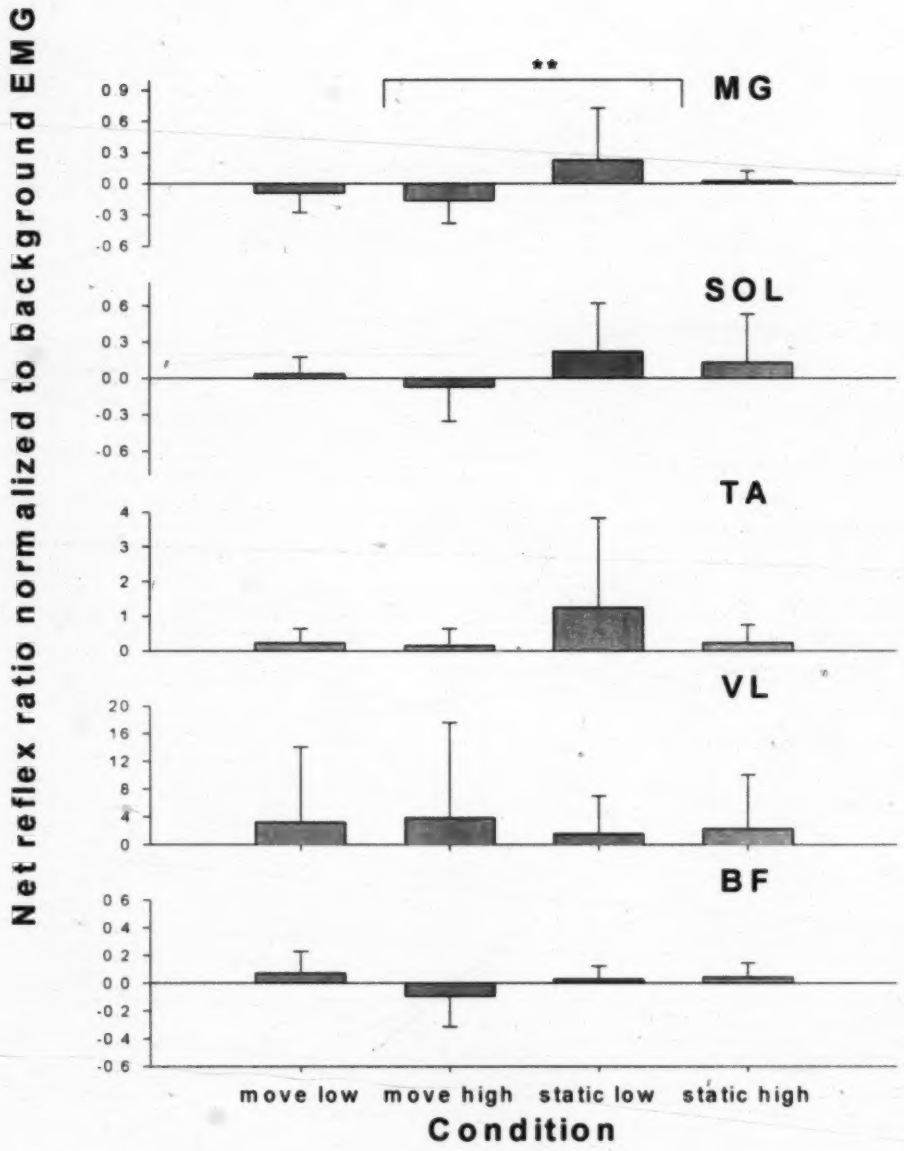


Figure 13– Experiment 2: Reflex ratio (net reflex/background EMG) for each movement condition. In MG, there was a reversal from inhibitory responses during movement, to excitatory responses during static contractions. The same pattern is observed in SOL, but was not statistically significant. Mean values are displayed with standard deviation.

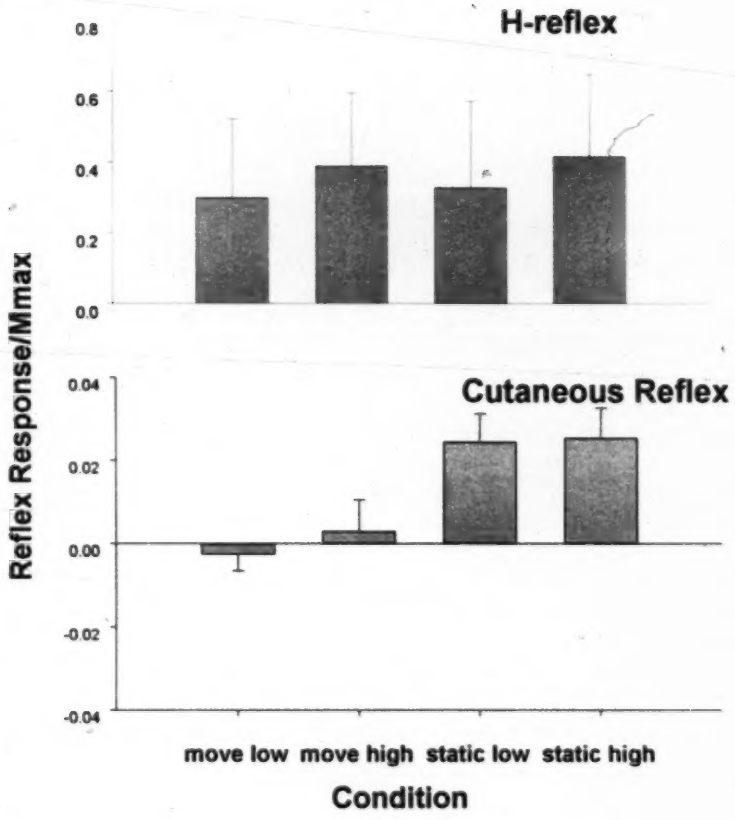


Figure 14: Comparison of SOL H- and cutaneous reflexes. H-reflexes are significantly larger in high versus low levels of background muscle activity, independent of movement type. Cutaneous reflexes, on the other hand, are significantly smaller during movement than during static conditions, regardless of background muscle activity.

VII. Glossary

Action potential: brief propagating depolarization of the axon; the basic unit of neuronal communication; the frequency of action potentials codes the intensity of a stimulus from a sensory ending or the intensity of muscular contraction from a motoneuron

Adaptation: the desensitization of a receptor to continuous input. A receptor will respond rapidly initially, then gradually fire at a lower frequency despite receiving the same intensity of stimulation

Anti-dromic: an action potential traveling in reverse to the normal direction of travel

Axon: the nerve fibre down which an action potential is propagated

Central Pattern Generator: Theoretical collective of neurons, assumed to be in the spinal cord, that generates coordinated, rhythmic activation of flexors and extensors to produce locomotion

Decerebrate: experimental preparation that leaves the spinal cord, brainstem and cerebellum intact, but disconnects the cortex and basal ganglia

Decorticate: as above, leaving the basal ganglia intact

Electromyography (EMG): a means of quantifying muscle activity, measuring levels of electrical activity in a selected muscle

Excitatory: any factor which produces a larger than normal response

Fictive locomotion: rhythmic firing of neurons that resembles that of firing patterns observed during true locomotion but does not result in movement of the limbs

Inhibitory: A factor which acts to make smaller or reduce the resultant effect when compared to results when the factor is not present

Interneuron: A neuron that can connect sensory and motoneurons, as well as connect to

other interneurons. Interneuronal connections are attributed with adding complexity to neuronal pathways, increasing the number of possible sites for excitatory and inhibitory synapses

GABA (gamma-aminobutryic acid): amino acid-based inhibitory neurotransmitter

Gain: the ratio of output to input. An increase in gain causes an increased output for a given input, while a decreased gain has the opposite effect.

Ischemia: a condition in which the blood flow to a limb or area of the body is occluded, often used to elicit a temporary reduction or abolition of Ia afference from the affected area.

MVC (Maximum Voluntary Contraction): the mean maximal force output (as quantified by EMG) that a muscle can generate, often used to normalize other measures of muscle activity

Nociceptive: a level of electrical stimulation, which activates high threshold pain receptors and thus is perceived as pain

Perceptual threshold (PT): minimum level of stimulus intensity at which stimulation is perceptible

Radiating threshold (RT): minimum level of stimulus intensity at which an electrical stimulus elicits a radiating parasthesia (tingling sensation at the site of stimulation that radiates along the path of the nerve); this value can be used to normalize experimental levels of stimulation (e.g., 2 x RT, 2.5 x RT)

Recurrent Inhibition: Produced by Renshaw cells, inhibitory interneurons located near the motoneurons in the ventral horns. Excited motoneurons have collaterals branching to the Renshaw cells, which in turn have inhibitory synapses on other nearby

motoneurons. Stimulation of one motoneuron thus tends to inhibit nearby motoneurons

Spinalize: transection of the spinal cord which removes the effects of any CNS area above the lesion from that below the lesion

Synapse: the junction between two neurons through which chemical neurotransmitters convey information from one neuron to the next